

Extension of a niche concept to spatially heterogeneous and time fluctuating ecological systems

Ph.D. dissertation

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Introduction

*“No concept in ecology has been more variously defined
or more universally confused than niche.”*

(L.A. Real and S.A. Levin, 1991)

Why do some species coexist whilst others do not? Why does the number of individuals in a population change within space and over time? What can enable a species to exclude another and what determines how many species are able to coexist within a given area? How stable is a coalition of species in a particular area? These are some of the questions, among many others, surrounding the basic issues of theoretical and community ecology. In our attempt to find the answers we believe that such questions should be approached by starting with simple systems before moving towards the more complex systems. Thus, as a starting point of our analysis, instead of choosing real, and therefore highly complex ecological systems, we shall proceed from simple mathematical models based on first principles. The focus of our investigation utilizes one of the central organizing concepts of modern community ecology, namely, the niche. This work extends the application of a mathematically correct definition of the niche which is usable in an ecological context to study populations in both structured and fluctuating environments.

Chapter 1

Basics of population dynamics and niche theory

1.1 The dynamics of unregulated populations

Ecological investigations, in most cases do not study specific individuals. Instead, they are concerned with a population i.e. individuals of a certain species (group, state, genotype, etc.) that live in a particular area. Our aim is to ascertain how the individual numbers of a certain population change within the space and over time. The present study makes use of a framework of strategic models (Czárán, 1998) which mostly apply a deductive approach. However, our investigation is based on a firm, model independent starting point which is the reproductive capacity of living organisms. Experience suggests (Malthus, 1789) that any population supplied with sufficient nutrition and favorable conditions will grow exponentially. In our approach we have chosen exponential growth as a reference point. Although the possibility for exponential growth is a simple mathematical consequence of the fact that life can only originate from life (see Eqs. (1.3) and (1.6)), nevertheless the usefulness of the approach can be questioned. It is certainly true that under natural conditions we rarely encounter exponentially growing populations: the density of a population is usually constant or fluctuating around a constant value. This fact, however, does not limit the fruitfulness of our approach. In classical mechanics it is also helpful, as a reference point, to conceive the behavior of a body in absence of a net force (see Newton's First Law of motion¹). This is also something which is rarely found in nature. Allocating such a special role to exponential growth raises the question of why most populations are not in that state and what can be behind the relative stability of population densities? Using an analogy between an unregulated (exponentially growing) population and a mechanical object moving in absence of a net force, we ought to look for the forces that prevent populations from growing ever larger. The “forces” that allow the population to stay in an intermediate level of abundance and more or less stabilize this state is the regulation, see Section 1.2.1.

The next sections present the basics of mathematical modeling of unregulated populations (both unstructured and structured), demonstrate the unavoidable role of regulation – the “force” that blocks the exponential growth – in describing populations and the connection between regulation and the concept of ecological niche.

¹Newton's First Law states that “Every object in a state of uniform motion tends to remain in that state of motion unless an external force is applied to it”.

1.1.1 Unstructured populations

As a first step in building the model we investigate the reasons for changes in the abundance of a population in a given location. The density can increase by birth and immigration and decrease by death and emigration (see Fig. 1.1). Since the number of births must be proportional to the current number of the present individuals (living organisms only originate from other living organisms) we can write the formal equation between the density of a population at time t and $t + 1$

$$N_{t+1} = N_t + \text{births}(N_t) - \text{deaths} + \text{immigration} - \text{emigration} \quad (1.1)$$

The equation above is too general to draw any conclusions from it as the factors in each ecological situation could be different, depending on parameters that are not indicated in Eq. 1.1. As a first step we should analyze the most simple but non

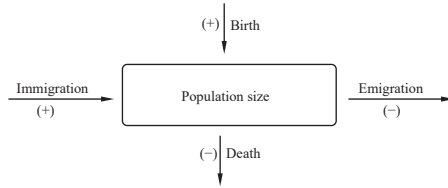


Figure 1.1: *Factors increasing (+) and decreasing (-) population size, cf. Eq. (1.1).*

trivial case in detail. We assume that the population is not spatially structured, i.e. that there is no immigration and emigration, and that the individuals are identical in all respects (for a sexual species we consider females only, assuming that an excess of males to ensure population growth is not constrained by mating chances). In the most simple case we find exponential growth in dynamic models (both in discrete and continuous time) of a simple unregulated population.

Assuming discrete time dynamics let the initial number (at $t = 0$) of individuals in the population be N_0 . In the first time step the change of the number of the individuals is the following

$$\Delta N_0 = N_0 \beta n - N_0 \delta = N_0 R, \quad (1.2)$$

where β is the fraction of the population that reproduce during that interval. The average number of the offspring is n , δ denotes the dying fraction of the population. In this model all these parameters are constant, independent of any circumstances, i.e. the system is unregulated. The per capita net rate of population growth is

$$R = \frac{\Delta N_0}{N_0} = \beta n - \delta,$$

which is a linear function of the actual population size. This important feature characterizes the growth of unregulated closed populations. The size of a population at $t = 1$ and at a given arbitrary T

$$N_1 = N_0 + \Delta N = N_0(1 + R) = N_0\lambda,$$

and

$$N_T = N_0(1 + R)^T = N_0\lambda^T, \quad (1.3)$$

where we introduced $\lambda = 1 + R$, the gross rate of population increase. As it is clear from these simple formulae, the number of individuals in a population having constant demographic parameters is an exponential function of time with a constant λ gross rate of growth. If λ is positive, negative or zero, the number of individuals increases, decreases or remains constant, respectively.

In the case of non-seasonally reproducing species continuous time models describe the system better. Let $N(t)$ be the number of the population at time² t , $r = b - d$, the difference of the birth and death rate for a sufficiently short period of time, the constant intrinsic per capita growth rate. The dynamic of the system is described by the following differential equation

$$\frac{dN(t)}{dt} = rN(t). \quad (1.4)$$

In separated form

$$\int_{N(0)}^{N(T)} \frac{dN(t)}{N(t)} = r \int_{t=0}^{t=T} dt, \quad (1.5)$$

after integration from $t = 0$ to $t = T$ and rearranging yields

$$N(T) = N(0)e^{rT}, \quad (1.6)$$

²According to the conventions we denote the time by indices and function notation, in case of discrete and continuous dynamics, respectively.

Box 1.1: Connection between discrete and continuous dynamics

Assume that a species reproduces at very short Δt time intervals. During the $0 \rightarrow T$ interval it reproduces $T/\Delta t$ times with a (discrete) rate of $r\Delta t$. The initial and final number of individuals are the following (cf. Eq. (1.3))

$$N_T = N_0 (1 + r\Delta t)^{\frac{T}{\Delta t}}. \quad (1.8)$$

Introducing $u = r\Delta t$, yields

$$N_T = N_0 (1 + u)^{\frac{T}{u}}. \quad (1.9)$$

The $u \rightarrow 0$ limit corresponds to the continuous time modeling. Since $\lim_{u \rightarrow 0} (1 + u)^{\frac{T}{u}} = e^{rT}$, the equation above can be written as

$$N_T = N_0 e^{rT}, \quad (1.10)$$

which is the same as Eq. (1.6) describing the continuous dynamics.

where $N(0)$ denotes the initial number of individuals. Note the simple connection between the parameters of the discrete and continuous growth:

$$(1 + R) = \lambda = e^r. \quad (1.7)$$

The connection between discrete and continuous time dynamics can be illustrated in another way, see Box 1.1

Although it is not obvious from the equations above, the exponential nature of growth is not altered even if the population has an arbitrary complex spatial structure (see Section 1.1.2, Caswell (2001)) or lives in a stationary fluctuating³ environment (see e.g. Tuljapulkar (1990); Turchin (2003)). In the latter case the density of populations fluctuates around the curve of exponential growth. The effect of demographic stochasticity caused by the stochastic behavior of birth and death

³The fluctuation of the environment is stationary if its status in every period can be characterized by a fixed distribution – this is not a strong restriction.

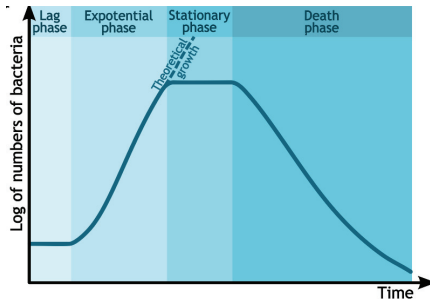


Figure 1.2: *The phases of bacterial growth. Lag phase ($r = 0$), log (exponential) phase ($r > 0$), stationary phase ($r \approx 0$), death phase ($r < 0$).*

processes could be significant only at very low densities. Based on these facts we can say that the capacity of exponential growth is a common feature and the “most natural” state of every population which consists of reproducible individuals. This is one of the central issues of population dynamics, that must be included in any ecological model or theory, and it is one of the cornerstones frequently referred to in this work.

However, exponentially growing populations are rarely observable – or for only short periods of time – in nature. The reasons for this can be found in the limited availability of resources, space and other environmental factors (see Section 1.2.1). The question arises as to how one can maintain this reference state for a long period; how can we sustain a population in the face of continuous exponential growth; how can we overcome the limits to growth caused by fast reproduction? The solution is shown with bacterial populations because of their short generation time. But we emphasize that all the following descriptions are valid for *any* other kind of populations, even if the experiments described below cannot be performed in practice.

Assume a bacterial population well supplied with nutrients. At the beginning the density of the population is approximately constant (lag phase). The population accommodates to the environmental conditions. After that the colony starts to grow exponentially (log phase) before it encounters a spatial or nutritional constraint. Then the log phase is followed by a stationery and a decreasing period due to the

Box 1.2: Phases of bacterial growth

Under ideal conditions, the growth of bacterial population has four different stages termed lag, log (exponential), stationary, and death. During *lag phase*, bacteria adapt themselves to growth conditions. It is the period where the individual bacteria are maturing and not yet able to divide ($r = 0$).

The *exponential phase* (sometimes called *log phase*) is a period characterized by cell doubling. The number of new bacteria appearing per unit time is proportional to the present population in this phase when metabolic activity is most intense and cell reproduction exceeds cell death ($r > 0$).

In the *stationary phase*, the growth rate slows down and the production of new cells equals the rate of cell death. This phase reflects a change in growing condition – for example, a lack of nutrients or the accumulation of waste products ($r \approx 0$).

When the rate of cell deaths exceeds the number of new cells formed, the population equilibrium shifts to a net reduction in numbers and the population enters the *death phase* ($r < 0$).

shortage of nutrients and space (death phase), see Figure 1.2 and Box 1.2. However, if we remove individuals continuously from the population during the log phase with a constant δ intensity – i.e. we dilute it – but ensure a continuous supply of the necessary well mixed nutrients, then the population continues to grow exponentially. The rate of growth can be tuned by the dilution rate Δ :

$$r - \Delta = 0. \quad (1.11)$$

This experiment can be performed in practice by a chemostat⁴ (Novick and Szilard, 1950) with microscopic organisms (bacteria, saccharomyces, planktonic algae, etc.). We underline that albeit we introduced this theory in connection with microscopic organisms, we can apply it to any kind of population as a *thought experiment*:

⁴The basic idea of the chemostat is linked with the name of Leó Szilárd, a Hungarian by origin physicist.

if we remove individuals from a population with a constant intensity, then the population remains continuously in the phase of exponential growth; the growth rate r can be set by the dilution rate Δ . This is also a central issue in our investigations and could help us to understand the necessity of population regulation.

1.1.2 Structured populations

The assumption that a population consists of identical individuals with same demographic parameters (i.e. the population is unstructured) is an extreme oversimplification. We extend our investigation to structured populations in which individuals belong to different classes (according to their ages, locations, size, genotypes, etc.) and these classes have different demographic parameters. The mathematical methods describing the system are different for discrete and continuous time. While such modeling often uses discrete time, we will apply a *continuous time* description because of its simpler-smoother behavior. (Some technical differences between the continuous and discrete time formalisms are discussed in Appendix A.) To simplify the formalism, we restrict our attention to a *finite number of individual states* – in most of the cases this is not a strong restriction.⁵

In this subsection we introduce the mathematical description for a single population with finite number of states in continuous time (see e.g. Caswell (2001) for details). It is assumed that individuals belong to one of the s different individual states (i-state, Metz and Diekmann, 1986). The vector

$$\mathbf{n} = \begin{pmatrix} n_1 \\ n_2 \\ \vdots \\ n_s \end{pmatrix}, \quad (1.12)$$

where n_j is the number of the individuals belonging to the individual state j , specifies the state of the population (p-state).

⁵In case of infinite dimensions the matrix formalism of this section is replaced by functional analysis. We do not deal with the problems of this treatment, see Diekmann et al. (1998, 2001, 2003) for details.

It can also be written as

$$\mathbf{n} = \tilde{n}\mathbf{p}, \quad (1.13)$$

where

$$\tilde{n} = \sum_{l=1}^s n_l \quad (1.14)$$

is the total population size and \mathbf{p} is the vector describing the population structure. Its generic element

$$p_l = n_l / \tilde{n}, \quad (1.15)$$

the p_l frequency of the state l is

$$\sum_{l=1}^s p_l = 1. \quad (1.16)$$

The continuous-time population dynamics is described by the matrix differential equation

$$\frac{d\mathbf{n}}{dt} = \mathbf{M}\mathbf{n}, \quad (1.17)$$

where the $s \times s$ matrix \mathbf{M} is the dynamical matrix. Its elements m_{jk} are the elementary demographic rates. Three processes contribute to these rates:

- Rate of birth of individuals belonging to state j by a parent of state k is a positive contribution to the element m_{jk} .
- Rate of death of individuals in state j is a negative contribution to the diagonal element m_{jj} .
- Rate of transition from state k to state j ($j \neq k$) is a positive contribution to the off-diagonal element m_{jk} and a negative one to the diagonal element m_{kk} .

The eigenvalues (ρ_j , $j = 1, 2, \dots, s$) and corresponding right and left eigenvectors (\mathbf{w}_j and \mathbf{v}_j , respectively) of the matrix \mathbf{M} are defined by the relations

$$\mathbf{M}\mathbf{w}_j = \rho_j\mathbf{w}_j \quad (1.18)$$

and

$$\mathbf{v}_j\mathbf{M} = \rho_j\mathbf{v}_j. \quad (1.19)$$

To get biologically interpretable results, we assume that the dynamical matrix \mathbf{M} has a simple⁶ and real dominant eigenvalue (defined as the eigenvalue with the largest real part), and the corresponding (dominant) left and right eigenvectors are real and strictly positive. These requirements correspond to the structure of the dynamical matrix. It is clear from definition above that all off-diagonal elements of the matrix are non-negative. Moreover, we assume that the matrix is irreducible, i.e. any states are reachable from any other, not necessarily directly (cf. Caswell, 2001, p. 81). According to a modified form of the Perron–Frobenius theorem, these properties guarantee that there is a simple and real dominant eigenvalue, the corresponding (dominant) left and right eigenvectors are real and strictly positive; see Appendix A for the proof.⁷

Without losing generality, we assume, that the dominant eigenvalue and the corresponding right and left eigenvectors are ρ_1 , \mathbf{w}_1 , \mathbf{v}_1 , respectively. The biological meaning of the dominant eigenvalue and eigenvectors becomes apparent from the following argument, which is a literal translation of its discrete-time equivalent (Caswell, 2001, p. 84). It is directly verifiable that the solution of the dynamics (1.17) is

$$\mathbf{n}(t) = \sum_{j=1}^s e^{\rho_j t} \gamma_j \mathbf{w}_j = e^{\rho_1 t} \left(\gamma_1 \mathbf{w}_1 + \sum_{j=2}^s e^{-(\rho_1 - \rho_j)t} \gamma_j \mathbf{w}_j \right), \quad (1.20)$$

⁶Because the speed of the convergence to the equilibrium distribution is determined by the difference between the largest and the second largest eigenvalue, if there are two (or more) dominant eigenvalues, there will be no relaxation in the system.

⁷Note that the non-negativity of the off-diagonal elements means that $-\mathbf{M}$ is a “Z-matrix” (Horn and Johnson, 1978). This fact implies a necessary and sufficient condition for the positivity of the growth rate. It is described by Hastings and Botsford (2006) for discrete time; the translation for the continuous case is straightforward.

where we used the following notation (the dot denotes scalar product)

$$\gamma_j = \mathbf{v}_j \cdot \mathbf{n}(0). \quad (1.21)$$

The left eigenvectors are normalized to satisfy the orthogonality relation:

$$\mathbf{v}_j \cdot \mathbf{w}_k = \delta_{jk} = \begin{cases} 1, & \text{for } j = k \\ 0, & \text{otherwise} \end{cases} \quad (j, k = 1, 2, \dots, s), \quad (1.22)$$

where the 'Kronecker-delta' notation was used.

For large t , the summation term of Eq. (1.20) diminishes. The population state becomes proportional to \mathbf{w}_1 and experiences an exponential growth with rate

$$r = \rho_1. \quad (1.23)$$

Positivity of \mathbf{w}_1 allows us to normalize it consistently with Eq. (1.16), i.e., as

$$\sum_{l=1}^s w_{1l} = 1. \quad (1.24)$$

Then we can state that

$$\mathbf{p} = \mathbf{w}_1 \quad (1.25)$$

holds after the initial relaxation. That is, the long-term growth rate and the equilibrated population structure is determined by the dominant eigenvalue and the dominant right eigenvector, respectively.

The coefficient

$$\gamma_1 = \sum_{l=1}^s v_{1l} n_l(0) \quad (1.26)$$

justifies referring to the j th element of the vector \mathbf{v}_1 as the “reproductive value” of the individual state j : any individuals contribute to the (exponentially growing) future population proportional to its reproductive value (Caswell, 2001, p. 93). We will use the notation

$$\mathbf{v} = \mathbf{v}_1 \quad (1.27)$$

for the vector of reproductive values; its generic element is $v_l = v_{1l}$.

1.2 Population regulation and niche

1.2.1 Unavoidable concept of regulation

As it is shown in the previous sections, in any population, in which the individuals are born and die independently of each other, i.e. if the population is unregulated, the density changes exponentially. The exponential growth sooner or later encounters obstacles. The most obvious one is the shortage of resources, but predation, spatial restraints, infections, and many other effects becoming stronger with the increasing density could be a limiting factor. These limiting factors regulate the growth of populations. Higher density of population causes a decrease in the available resources, the competition becomes stronger, the predation pressure increases, the effects of spatial restraint become considerable. As a consequence, the growth rate of the population decreases and reaches or fluctuates around zero. The notion of regulation should be extended over the well-known resource limitation. All the factors that prevent the population from exponential growth are regulating the growth. Thus, the regulating variables (regulating factors, (Krebs, 2001; Case, 2000); environmental interaction variables, environmental variables, (Heino et al., 1997), (Diekmann et al., 2003, 2001)), are the set of variables by which the feedback of the population regulation operates. These depend on the population density and affect some of the demographic parameters of the individuals. For notational convenience we collect the regulating variables into a vector $\mathbf{I} = \mathbf{I}(n)$, which is a function of population sizes. The number of the elements of this vector (i.e. the dimension of the vector) is the dimension of the population regulation. Beyond the regulating variables, demographic parameters are affected by external parameters that are independent of the present state of the population, thus they are not the part of the regulation loop. These are called external environmental parameters and collected into vector \mathbf{E} . Such variables are e.g. temperature, humidity or stress. As a matter of definition, vectors \mathbf{I} and \mathbf{E} completely describe the affect of the external environment and other populations on demography, see Fig. 1.3. Specifically \mathbf{I} describes all interactions between the individuals. Using Turchin (2003) terminology \mathbf{I} and \mathbf{E} are the vectors of endogenous and exogenous parameters, respectively.

In every (biological) system robust coexistence is made possible by the internal

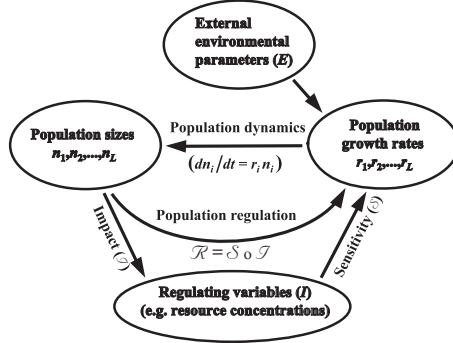


Figure 1.3: *The schema of population regulation. Population dynamics is governed by the growth rates. These growth rates depend on the sizes of the populations via the regulation loop \mathcal{R} . The population regulation is mediated through regulation variables collected in I . The external environmental parameters, collected in vector E , are not involved in the regulation loop. These variables act on the demographic parameters but not affected by the population sizes. (Figure from Meszéna et al. (2006))*

feedbacks (stabilizing mechanism, Chesson (2000b)). This feedback, in our case the population regulation, controls the birth and death rates in such a way that these result in zero net growth rate under different external environmental parameters (E). The range of E that allows regulation to operate in this manner, should be not too narrow. If the population regulation is weak, small changes in external parameters could result in large changes in the population sizes, driving the population into extinction or to verge of extinction. Consequently if the population regulation is weak or zero, the robustness of coexistence is weak or zero as well. For precise mathematical explanation see Chapter 2.

The following is an example of the unavoidability of population regulation. Assume that a population has been surviving for 10,000 years. Let $N(0)$ and $N(t)$ be the number of individuals in the beginning and at the end of the time interval, respectively.

Then the growth rate averaged over 10,000 years is the following (cf. Eq. (1.6)):

$$r = \frac{\ln \frac{N_T}{N_0}}{T}.$$

Assume that the initial and final densities are of the same magnitude, i.e. $0,1 < \frac{N_0}{N_T} < 10,0$. Then one can conclude that

$$|r| < 0.00023.$$

Obviously it is completely unlikely that the growth rate of a population approximates to zero “by itself”, without regulation. Thus, population regulation must be the central issue of any ecological theory, although its empirical demonstration is hard or nearly impossible in many real ecological systems.

1.2.2 Niche: address and profession, impact and sensitivity

Niche is one of the fundamental concepts of ecology. While it is often used in every field of ecology, its meaning is not always consistent with the underlying assumptions and principles. According to its central status it was variously defined by many different authors, see e.g. Chase and Leibold (2003) for a detailed overview. The '70s and '80s was the “golden age” of niche theory. In this period about 25% of the articles published in journal *Ecology* contain the word ‘niche’, but it also appears that current decade could see the renaissance of this concept, see Fig. 1.4.

However, the debate over the role, necessity and definition of niche – with varying intensity – has continued so far. The opinions are often very polarized: “I think it is good practice to avoid the term niche whenever possible” (Williamson, 1972)); or “... the theory of niche helps us to understand fundamental questions of ecology” (Schoner, 1989)). As a result of this debate, the term “niche” was not precisely defined in ecology. Its most accepted meaning could be summarized (temporarily and intentionally in a rough-and-ready way) as follows: Niche is a subset of the space of ecological roles and possibilities that is occupied by a species. The token of its coexistence is partitioning of this space amongst each other, i.e. in each “niche” there is only one species.

It is not our subject to give an overview of the evolution of the concept of niche. Instead, we introduce a possible interpretation of niche as a theoretical basis and

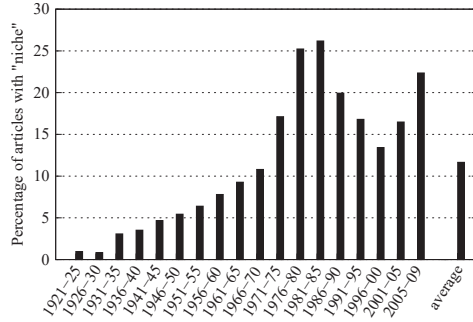


Figure 1.4: *Percentage of articles in Ecology that contained the word “niche”. Data from www.jstor.org and esapubs.org. Original graph from Chase and Leibold (2003, p. 3) extended with the data of the last decade.*

framework of a robust mathematical model (Chapter 2) according to Meszén et al. (2006): the notion of impact and sensitivity niche. The starting point is the reproductive capacity again: an unregulated population is in the phase of exponential growth, no matter how complex, spatio-temporally heterogeneous the environment is (Chapter 1.2.1). The growth of increasing populations sooner or later meets with some kind of obstacle. If two (or more) species are similar to each other, they have the same regulating factors (Darwin, 2001 p. 70). If they are completely similar in sense of growth limitations, their coexistence is impossible⁸. This is the fundamental concept of the principle of competitive exclusion. The basic condition of the coexistence of species is ecological differentiation. In this work we use the notion of competition in its “wide” meaning, and do not restrict the use to resource competition, albeit in relevant literature niche and resource competition are falsely but strongly entangled. As Chase and Leibold (2003, p. 11) show “[...] both Hutchinson and MacArthur also considered many other factors [*in addition to competition for resources*] such as predation and environmental variability, subsequent authors focused in their work on resource competition. The word ‘niche’ became firmly entangled with the notion

⁸More precisely it is absolutely unlikely, because this coalition is extremely sensitive towards external environmental parameters, see Section 1.2.1

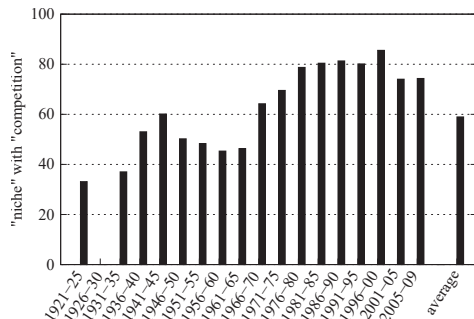


Figure 1.5: Percentage of articles containing the word “niche” that also contained the word “competition”. Data were obtained as in Fig. 1.4 Original graph from Chase and Leibold (2003, p. 12) extended with the data of the last decade.

of interspecific competition”, see Fig. 1.5. We have found⁹ no strong correlation between usage of the term “niche” and two other common species interactions, namely mutualism (10–20%) and predation (20–40%).

Different species can coexist if their growth meets with different regulating variables. The collection of these factors is the abstract niche space, which must be partitioned by species amongst each other. This ecological segregation can be realized in two ways (Miller, 1967). If the environmental requirements of species are different, they live in a spatially separated way, this type of segregation could be called *address niche*. This is a connection between the space of environmental conditions and the geographical space that shows, under which conditions the species are viable. We can distinguish two types of address niche: the fundamental and the realized one. The first one is the range of environmental requirements in which a species can survive. The second one is a narrower range where we can find the species as a result of the competition. However the species could segregate because of the different kind of resource limitations, in spite of living at the same location. This type of niche could be termed as *profession niche*. The distribution of species in the ecological space can be described by the address and profession niche together. Thus, the

⁹Data were obtained as in Fig. 1.4

regulating factors must be partitioned in this way, e.g. a given resource must be considered according to its utilizability and geographical occurrence. If the segregation is realized either by address or profession two (or more) species can coexist, because they are not in competition¹⁰. Different terminology, “Eltonian” and “Grinnelian” niche (or “scenopoetic” and “bionomic” niche axes in continuous case) is often used for address and profession niche, respectively (Leibold, 1995; Hutchinson, 1978).

There is another, independent way of partitioning the niche, based on the number of elements of niche space. If the number of regulating variables is finite (e.g. three different resources or five habitats) then the niche space is discrete. If the regulating factors form a continuous manifold (e.g. temperature, size of a resource) these factors form the niche space. Because the maximal number of coexisting species should not exceed the number of resources, in a discrete niche space the maximal number of coexisting species is the number of the elements of the niche space. In the case of a continuous niche space this is seemingly not a valid restriction, therefore this approach needs some refining.

The regulating capability of a given resource toward a species is usually characterized by the resource utilization function (RUF). If a resource is a more important regulating factor, the value of RUF is higher at this resource. The competition between two species can be measured by the “overlapping integral” between the two RUFs: the larger they overlap the higher competition. This approach solves the problem of the continuous niche space and of the number of maximal coexisting species. Although the resource utilization function is a widespread and commonly used term in ecology (in most cases a niche of a species is usually specified by its “resource utilization”), it is a phenomenological term; there is no unequivocal method of measuring it, and it is almost impossible to use in describing real ecological situations.

It is appropriate to define the niche in such a model in an model independent way that can be used in finite and infinite dimensions, show the strength of the population regulation (i.e. the robustness of the coexistence) and can be determined in real ecological situations more easily than RUF. To this end (according to Meszéna

¹⁰It is noticeable in the literature that the address niche is more frequently used in the empirical investigation because it is easy to measure, while the profession niche dominates in the theoretical work, as it is easy to model because of the lack of spatiality.

et al. (2006)) we decompose the population regulation into two parts¹¹ (cf. Fig. 1.3) to separate the effect of the population on the regulating factors and the effect of regulating factors on demographic parameters. Let us define the ecological role of a species as the following:

- the *sensitivity* of a species means the change of the growth rate of the species as a result of small changes of a given regulating factor
- the *impact* of a species means the change of a given regulating factor as a result of small changes of population sizes

The issue of impact and sensitivity niche is a generalization of the resource utilization function¹². Naturally, a species consumes and depends on those resources on the whole that it can utilize. The difference is that impact and sensitivity are well-defined quantities in contrast to RUF. The niche of a species can be determined by giving its impact on and sensitivity towards the regulating factors.

Chapter 2 as a summary of Meszéna et al. (2006) introduces this concept of niche in a mathematical way and proves in a model-independent way that increasing similarity between the populations makes their coexistence less likely, i.e. more sensitive to the perturbation of external parameters. Chapter 3 shows the applicability of the theory to spatial niche segregation in heterogeneous environment. Chapter 4 presents model studies by analyzing applicability of this theory on patchy environment. In Chapter 5 we investigate the usefulness of this approach in fluctuating environment.

¹¹There are many other possible ways of decomposition, but for describing ecological systems this is the most natural way.

¹²Note that the niche theoretical relevance of the two-way interaction between a population and its environment was first emphasized by Leibold (1995)

Chapter 2

Background: Limiting similarity and niche in unstructured populations

This chapter is based on the article:

G. Meszéna, M. Gyllenberg, L. Pásztor, J. A. J. Metz: *Competitive exclusion and limiting similarity: a unified theory*. Theoretical Population Biology 69(1), 68-87 (2006)

2.1 A mathematical model of niche for unstructured population

Using the concept of the decomposition of the population regulation introduced in Section 1.2.1 we formulate the theory in a strict mathematical way by introducing niche vectors and analyzing the robustness of coexistence for unstructured populations. We restrict our attention to unstructured population of L coexisting species, where the state of the community can be described only by the population sizes $n^{(1)}, n^{(2)}, \dots, n^{(L)}$ (the i th population is distinguished by the superscript (i)). According to the decomposition of the regulation loop (Fig. 1.3), the population sizes determine the values of the regulating variables:

$$\mathcal{I} : \quad (n^{(1)}, n^{(2)}, \dots, n^{(L)}) \rightarrow \mathbf{I} = \mathcal{I}(n^{(1)}, n^{(2)}, \dots, n^{(L)}). \quad (2.1)$$

Map \mathcal{I} is the *impact function* (or *output map* in the terminology of Diekmann et al., (2001,2003)) of the system. As a matter of definition, we assume that *all* interactions between the individuals are channeled through D “regulating variables” collected into the D dimensional vector \mathbf{I} (for example resource, predation, infection, etc.). These regulating variables via the map \mathcal{S} determine the growth rates of the population at a given \mathbf{E} ($r^{(i)}$ denotes the growth rate of species i):

$$\mathcal{S} : \quad \mathbf{I} \rightarrow (r^{(1)}(\mathbf{I}, \mathbf{E}), r^{(2)}(\mathbf{I}, \mathbf{E}), \dots, r^{(L)}(\mathbf{I}, \mathbf{E})). \quad (2.2)$$

We will refer the relation \mathcal{S} as the *sensitivity function*. Note that external environmental factors (\mathbf{E}) are exogenous parameters affect the growth rate of the populations but are not affected by the population sizes (stress, temperature, humidity, etc.), see Section 1.2.1. As a consequence of the definition the vectors \mathbf{E} and \mathbf{I} (limiting factors) completely describe the environment affecting the demographic parameters.

The composition of the impact and sensitivity map determines the population regulation \mathcal{R} :

$$\mathcal{R} = \mathcal{S} \circ \mathcal{I} : \quad (n^{(1)}, n^{(2)}, \dots, n^{(L)}) \rightarrow (r^{(1)}(\mathbf{I}, \mathbf{E}), r^{(2)}(\mathbf{I}, \mathbf{E}), \dots, r^{(L)}(\mathbf{I}, \mathbf{E})), \quad (2.3)$$

that is the dependence of the growth rates on the population sizes at a given fixed \mathbf{E} .

Then the population regulation determines the dynamics of the population:

$$\frac{1}{n^{(i)}} \frac{dn^{(i)}}{dt} = r^{(i)}(\mathcal{I}(n^{(1)}, n^{(2)}, \dots, n^{(L)}), \mathbf{E}) \quad (i = 1, 2, \dots, L). \quad (2.4)$$

The requirement of coexistence of L species is the zero growth rates:

$$r^{(i)}(\mathcal{I}(n^{(1)}, n^{(2)}, \dots, n^{(L)}), \mathbf{E}) = r^{(i)}(\mathbf{I}, \mathbf{E}) = 0 \quad (i = 1, 2, \dots, L). \quad (2.5)$$

Note, that the effect of the population sizes on the regulating variables is not necessarily instantaneous. However, we need to specify only the equilibrium equations; $\mathbf{I}(n^{(1)}, \dots, n^{(L)})$ represents the equilibrium value of vector \mathbf{I} at population sizes $n^{(1)}, n^{(2)}, \dots, n^{(L)}$. This system consists of L equations for $\dim \mathbf{I} = D$ unknowns. Generically $L \leq D$ must be satisfied for the existence of community. Coexistence of L population requires L different regulating mechanisms to adjust all population sizes for equilibrium when all growth rates are zero. A solution may exist if $L > D$ (when there are more species than regulation variables), but these solutions are structurally unstable. Such unregulated equilibrium disappears suddenly if, by whatever reason, an arbitrary small additional change in the external parameters starts to affect some, but not all populations.

From this result, one can state the “discrete” version of the competitive exclusion principle: the structurally stable coexistence of L population requires population regulation of dimension more than or equal to L (MacArthur and Levins, 1964; Rescigno and Richardson, 1965; Levin, 1970; Armstrong and McGehee, 1980; Heino et al., 1997). Note that in such case when a change in the external environment does not modify the feedback loop, the elements of \mathbf{E} are parameters rather than unknowns, should not be taken into account as regulating factors, consequently does not affect the maximal number of coexisting species.

2.2 Limiting similarity and niche

Below we demonstrate that robustness of coexistence requires sufficient difference between the populations in their relationship with the regulating variables. Differentially, the interaction between the populations and the regulating variables is characterized by two vectors,

$$\mathbf{C}^{(i)} = \frac{\partial \mathbf{I}}{\partial n^{(i)}} \quad \text{and} \quad \mathbf{S}^{(i)} = -\frac{\partial r^{(i)}}{\partial \mathbf{I}} \quad (i = 1, 2, \dots, L), \quad (2.6)$$

together describing the ecological role of the i th population. They will be referred to as *impact* and *sensitivity* niche vectors, respectively. One can write them also in the component-wise form

$$C_k^{(i)} = \frac{\partial I_k}{\partial n^{(i)}}, \quad S_k^{(i)} = -\frac{\partial r^{(i)}}{\partial I_k}, \quad (i = 1, 2, \dots, L; \quad k = 1, 2, \dots, D). \quad (2.7)$$

The quantities $C_k^{(i)}$ and $S_k^{(i)}$ measure the i th population's impact on and sensitivity towards the k th regulating factor, respectively. The sign convention for the sensitivity corresponds to the case when the regulating variables describe the *deterioration* of the environment, e.g. the exploitation of the resources. (Box 2.1 provides an example for calculating niche vectors for a specific model.)

The community matrix is defined as the derivative of the population regulation \mathcal{R} (cf. Eq. (2.3)):

$$a_{ij} = -\frac{\partial r^{(i)}}{\partial n^{(j)}}, \quad (2.14)$$

where we suppress the n dependence of r . The element a_{ij} of the community matrix measures the sensitivity of the growth rate of population i to a small change in the size of the j th population. Using the chain rule we can establish a connection between the (differential) community matrix and the (differential) niche vectors as the following

$$a_{ij} = -\frac{\partial r^{(i)}}{\partial n^{(j)}} = \sum_{k=1}^D S_k^{(i)} C_k^{(j)} = \mathbf{S}^{(i)} \cdot \mathbf{C}^{(j)} \quad (i, j = 1, 2, \dots, L). \quad (2.15)$$

To analyze the robustness of coexistence imagine a situation in which sufficient number of regulating factors are present, but some of them are very similar to each other from the point of view of the species (see Abrams (1988) for an analysis of this problem). This is an intermediary situation between having, or not having L independent regulating mechanisms. Alternatively, assume that the regulating factors itself are different enough, but the species are not, again leading to the situation in which the existence of L different regulations is in doubt. Then the community

Box 2.1: Niche vectors in Tilman's model

In a more specific version of Tilman's model L species compete for D resources, and their combined dynamics is the following (Tilman, 1982; Meszéna et al., 2006):

$$\frac{1}{n^{(i)}} \frac{dn^{(i)}}{dt} = r^{(i)} = f^{(i)}(R_1, R_2, \dots, R_D) - m^{(i)} \quad (2.8)$$

and

$$\frac{dR_j}{dt} = a(R_j^0 - R_j) + \sum_{i=1}^L c_j^{(i)} n^{(i)}, \quad (2.9)$$

where R_j is the availability of resource j ; $m^{(i)}$ is the species specific mortality; $c_j^{(i)}$ is a simplified form of the per capita resource consumption.

At fixed densities the resource equilibrium points can be calculated as

$$R_j^* = R_j^0 - a^{-1} \sum_{i=1}^L n_j c_j^{(i)}. \quad (2.10)$$

The regulating variables can be defined as the resource depletion

$$I_j = R_j^0 - R_j = a^{-1} \sum_{i=1}^L n^{(i)} c_j^{(i)} = \sum_{i=1}^L n^{(i)} C_j^{(i)}, \quad (2.11)$$

where the components of the impact niche vector are

$$C_j^{(i)} = a^{-1} c_j^{(i)}. \quad (2.12)$$

The sensitivity niche vector is

$$S_j^{(i)} = -\frac{\partial r^{(i)}}{\partial I_j} = \frac{\partial f^{(i)}}{\partial R_j}. \quad (2.13)$$

is regulated, but weakly. It has some tolerance towards the changes in external parameters, but only a weak one. While an infinitesimal additional mortality does not destroy coexistence, a small one does.

Implicit differentiation of the set of equilibrium equations (Eq. (2.5)) gives the sensitivity of the densities toward the external parameters

$$\frac{\partial n^{(i)}}{\partial \mathbf{E}} = \sum_{j=1}^L (a^{-1})_{ij} \frac{\partial r^{(i)}}{\partial \mathbf{E}} = \frac{1}{J} \sum_{j=1}^L \text{adj}(a)_{ij} \frac{\partial r^{(i)}}{\partial \mathbf{E}}, \quad (2.16)$$

where $\text{adj}(a)$ denotes the adjunct matrix. The determinant

$$J = \det(a_{ij}) \quad (2.17)$$

measures the strength of the regulation on the community level.

If $|J|$ is small, i.e. if the community is weakly regulated, Eq. (2.16) predicts strong dependence of the population sizes on the extra mortalities. In this case the equilibrium population size is very sensitive to the change of the external parameters, a small change in \mathbf{E} could drive some of the populations into extinction. Therefore, when J is small the coexistence is not robust, a fine tuning of the parameters is needed to achieve coexistence. If $J = 0$ (which includes the case $L > D$), matrix a is not invertible. Then, there exists an \mathbf{E} that cannot be compensated by a change of the population sizes. That is, coexistence is structurally unstable.

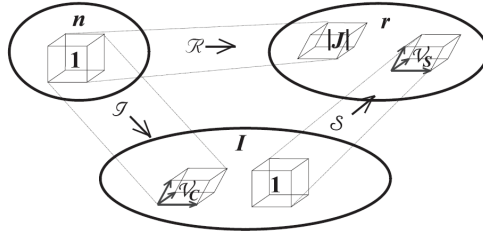


Figure 2.1: *Volume measures of the population regulation.* (Figure from (Mészéna et al., 2006))

There is a connection between J , the measure of the strength of the population regulation and the impact and sensitivity niche vectors $\mathbf{C}^{(i)}$ and $\mathbf{S}^{(i)}$. $|J|$ is the volume of the image of the unit cube under map \mathcal{R} , this/ is the measure of the population regulation. A similar measure can be setting up for the impact map \mathcal{C}

and the sensitivity map \mathcal{S} . The impact function \mathcal{C} maps the unit cube to an L -dimensional parallelepiped with volume¹ \mathcal{V}_C , spanned by the impact vectors $\mathbf{C}^{(i)}$. Analogously, the sensitivity function \mathcal{S} maps the unit cube into a parallelepiped with volume \mathcal{V}_S , spanned by the sensitivity niche vectors $\mathbf{S}^{(i)}$ (see Fig 2.1). The connection between the regulation strength and the niche vectors is the following (for the proof, see Meszéna et al. (2006)):

$$|J| \leq \mathcal{V}_C \cdot \mathcal{V}_S. \quad (2.18)$$

Volumes \mathcal{V}_C and \mathcal{V}_S measure the dissimilarity of the impact and sensitivity niche vectors in linear sense. The larger dissimilarity (in linear sense) between $\mathbf{C}^{(i)}$ vectors the larger volume of \mathcal{V}_C . In the special case when $\mathbf{C}^{(i)}$'s are (linearly) dependent then $\mathcal{V}_C = 0$. Analogous argument holds for \mathcal{V}_S and the sensitivity niche vectors. Therefore all the impact niche vectors and all the sensitivity niche vectors should be different enough – population have to differ both in their effects on the regulating variables and in their dependence on these variables – to achieve structurally stable coexistence. Diminishing difference between the niche vectors leads diminishing likelihood of coexistence.

To simplify our formalism we assume that the external parameters act as an extra mortality on i th population (cf. Eq. 2.5):

$$r^{(i)}(\mathbf{I}, \mathbf{E}) = r^{(i)}(\mathbf{I}) - \Delta^{(i)}. \quad (2.19)$$

Negative values of $\Delta^{(i)}$ represent decreased mortalities.

In the latter if we use $r^{(i)}$ without arguments it stands for $r^{(i)}(\mathbf{I})$. With this simplification the equilibrium conditions can be read as

$$r^{(i)}(\mathbf{I}(n^{(1)}, n^{(2)}, \dots, n^{(L)})) - \Delta^{(i)} = 0 \quad (i = 1, 2, \dots, L). \quad (2.20)$$

For tractability we collect the variables $n^{(i)}$, $r^{(i)}$ and $\Delta^{(i)}$ in the vectors \mathbf{n} , \mathbf{r} and $\mathbf{\Delta}$, respectively. The probability distribution of the external environmental parameters represented by a probability density of the mortalities $p(\mathbf{\Delta})$.

¹Note, that these volumes are not determinants, because the dimensionality before and after the mapping is not necessary the same.

Then the probability $P(\mathbf{n} > 0)$ of having all equilibrium densities positive satisfies

$$P(\mathbf{n} > 0) = \int_{\mathbf{n} > 0} \frac{p[\mathbf{r}(\mathbf{n})]}{k[\mathbf{r}(\mathbf{n})]} |J(\mathbf{n})| d\mathbf{n}, \quad (2.21)$$

where $k[\rho]$ denotes the number of all positive \mathbf{n} values for which $\rho = \mathbf{r}(\mathbf{n})$ (see (Rado and Reichelderfer, 1995)).

Obviously, according to Eq. (2.21) the probability that all L species coexist goes to zero when $|J(\mathbf{n})| \rightarrow 0$ for all relevant \mathbf{n} . The probability of finding the suitable conditions (external parameters, additional mortalities) for coexistence is small if $|J|$ is small.² The coexistence is considered robust if the fixed point exists and remains in the positive range for a wide range of $\Delta^{(i)}$ s. For the sake of explanation, assume that the extra mortalities are uniformly distributed random variables. Then, the probability of coexistence is proportional to the volume of $\Delta^{(i)}$ s that allows coexistence. We will analyze the robustness of coexistence in the next chapters in this sense.

Our results can be summarized as the *Limiting similarity Principle* (from Meszéna et al. (2006)) “Any of the following conditions imply the next one and make the coexistence of a given set of populations improbable, i.e. restricted to a narrow range of the external environmental parameters:

- Large overlap between either the impact or the sensitivity niches.
- Small \mathcal{V}_C or \mathcal{V}_S .
- Small $|J|$ ”

²Note that the probabilistic treatment does not assume any stochasticity in the behavior of the populations.

Chapter 3

Limiting similarity for structured populations

This chapter is based on the article:

A. Szilágyi, G. Meszéna: *Limiting similarity and niche theory for structured populations*. Journal of Theoretical Biology 258, 27-37 (2009)

Introduction

The main limitation of the formalism of Meszéna et al. (2006) was that it considered the populations to be homogeneous. In reality, individuals may belong to different states according to their age, size, developmental/physiological state, or location. Conspecific individuals in different developmental states often assume different ecological roles, making the notion of the niche of a structured population non-trivial.

Spatial structure has a pronounced importance for niche theory also. Living in different habitats, under different environmental conditions, eliminates competitive exclusion, just like if they were consuming different resources, or differ in ecological function in any other way. These two essential ways of niche segregation will be referred to as habitat and functional segregation see Section 1.2.2 (and cf. the “scenopoetic” and the “bionomic” niche axes of Hutchinson, 1978, p. 159). As different habitats are located at different places, description of a habitat-type niche segregation, unlike a functional one, necessitates to take into account the spatial structure of the populations in a heterogeneous environment.

Fortunately, there is a general mathematical way of handling any type of population structure. While the demographic parameters tend to differ in the different states, the long-term behavior of the population can be described by a single rate of increase, calculable as the leading eigenvalue of the dynamical matrix (Metz and Diekmann, 1986; Metz et al., 1992; Caswell, 2001). In this chapter we establish niche theory of structured populations by connecting the population-level niche description to the description of the individual states. We will assume that all individual states are reachable from all others (i.e. irreducibility). The more special case of spatial structure will receive special attention. This chapter develops the theory in general as well as for the spatial case.

3.1 The general theory

The overall growth rate of the population is calculable from the matrix elements, i.e. from the demographic parameters of the i -states. In the same spirit, we intend to determine the overall impact and sensitivity niche vectors of structured populations based on the impact and sensitivity parameters of the i -states and then we should

demonstrate that this overall niche description does provide the limiting similarity conclusion in line with the unstructured case. As a first step instead of Eq. (2.20) we should write the equilibrium equation in the following form

$$\frac{d\mathbf{n}^{(i)}}{dt} = \left[\mathbf{M}^{(i)}(\mathbf{I}(\mathbf{n}^{(1)}, \mathbf{n}^{(2)}, \dots, \mathbf{n}^{(L)})) - \Delta^{(i)}\mathbf{1} \right] \mathbf{n}^{(i)} = \mathbf{0}, \quad (3.1)$$

where $\mathbf{1}$ denotes the identity matrix.

Note the analogy to the chemostat. The rate of excess mortality $\Delta^{(i)}$ can also be seen as a (species-dependent!) removal, or dilution rate. This way, our equilibrium population can be seen as an exponentially growing one with the tunable growth rate $\Delta^{(i)}$ (cf. Section 1.1.1). Accordingly, the equilibrium p-state vector of species i is an eigenvector of its dynamical matrix $\mathbf{M}^{(i)}$ with the (leading) eigenvalue $\Delta^{(i)}$. As the equilibrium is affected by the dilution rates, changing $\Delta^{(i)}$ s result in perturbation of the population structures. Importantly, the dynamical matrix should be evaluated at the equilibrium values of the regulating variables, affected by the dilution rate.

Our first job is to build the connection between this $L \times s$ dimensional dynamical system and the L dimensional case of unstructured populations. The only thing, we are interested in, is whether the populations survive the extra mortalities (see Eq. (2.21) and the following paragraph). From this point of view, the $\tilde{n}^{(i)}$ s are the only relevant parameters. When the L dilution rates are tuned, the equilibrium point of dynamics (3.1) moves on an L dimensional submanifold of the $L \times s$ dimensional state space (Fig. 3.1). This manifold can be parameterized also by the L equilibrium total population sizes $\tilde{n}^{(1)}, \tilde{n}^{(2)}, \dots, \tilde{n}^{(L)}$.

With this variable change, one can consider the equilibrium \mathbf{I} as a function of the $\tilde{n}^{(i)}$ s:

$$\mathbf{I} = \hat{\mathbf{I}}(\tilde{n}^{(1)}, \tilde{n}^{(2)}, \dots, \tilde{n}^{(L)}). \quad (3.2)$$

Moreover, the growth rate (the dominant eigenvalue of the dynamical matrix) can be written as a function of the regulating variable:

$$r^{(i)} = r^{(i)}(\mathbf{I}). \quad (3.3)$$

Eqs. (3.2-3.3) establishes a description that is isomorphic to Eq. (2.20).

A note of precision is needed here. The equilibrium point of dynamics (3.1) at a given dilution rate is not necessarily unique. However, as we consider a stable

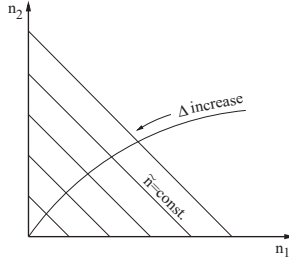


Figure 3.1: *Dimension reduction.* The two axes represents $n_1^{(i)}$ and $n_2^{(i)}$, i.e. the number of individuals in two i -states of one of the species. Under changing one of the excess mortalities the equilibrium point moves on a curve. (In the figure the species' own mortality is tuned, so the curve follows the fate of that population until extinction.) The curve can be parameterized also by the total population size $\tilde{n}^{(i)}$. The $\tilde{n}^{(i)} = \text{constant}$ points lie on a straight line of -45° direction.

fixed point, implicit function theorem guaranties that the equilibrium point is *locally* unique and is a smooth function of the $\Delta^{(i)}$ s. We assume that the local map $(\Delta^{(1)}, \dots, \Delta^{(L)}) \rightarrow (\tilde{n}^{(1)}, \dots, \tilde{n}^{(L)})$ is invertible. (Recall that non-invertibility would mean structural instability of the coexistence.) This inversion allows us to locally parameterize the manifold by the total population sizes, leading also to the locally unique mapping (3.2).

According to Section 1.1.1, in a *thought experiment* one can apply any combination of extra mortalities (the $\Delta^{(i)}$ s) to the populations and observe the correlated change of the equilibrium population sizes of the species and the regulating variables. From this data set one can reconstruct the functions $r(\mathbf{I})$ and $\mathbf{I}(n_1, n_2, \dots, n_L)$.

Based on this reduction of the number of variables, now we have to build the quantitative connection between the robustness analysis for the structured and for the unstructured descriptions.

We begin the work with the sensitivity side: How does the population growth rate depend on the regulating variables? On the i -state level, our starting point is the sensitivity of the elementary demographic rates which is considered to be known

from the model definition. It can be described by the linear operator $T_{jkm}^{(i)}$

$$dM_{jk}^{(i)} = - \sum_{m=1}^D T_{jkm}^{(i)} dI_m \quad (j, k = 1, 2, \dots, s), \quad (3.4)$$

where $dM_{jk}^{(i)}$ is the change of the i th population matrix under the perturbation dI_m of the regulating variables. The operator can be determined via differentiating the map $\mathbf{M}^{(i)}(\mathbf{I})$, which is considered given by the model definition. Like in Eq. (2.6), the minus sign corresponds to the depletive interpretation of the regulating variables.

The change of the population growth rate is determined by the perturbation of the dynamical matrix as (Caswell, 2001, Appendix B)

$$dr^{(i)} = \sum_{j,k=1}^s v_j^{(i)} dM_{jk}^{(i)} p_k^{(i)}. \quad (3.5)$$

That is, the perturbation of the $k \rightarrow j$ rate contributes to the change of the population growth rate proportional to the frequency p_k of initial state k and to the reproductive value v_j of the final state j .

Comparison of Eq. (3.5) with the definition (2.7) leads to the identification

$$\sum_{m=1}^D S_m^{(i)} dI_m = \sum_{j,k=1}^s \sum_{m=1}^D v_j^{(i)} T_{jkm}^{(i)} dI_m p_k^{(i)}. \quad (3.6)$$

That is, the sensitivity vector can be written as

$$S_m^{(i)} = \sum_{j,k=1}^s v_j^{(i)} T_{jkm}^{(i)} p_k^{(i)} \quad (m = 1, 2, \dots, D). \quad (3.7)$$

Interpretation is inherited from the perturbation result (3.5). Sensitivity of a population towards the regulating variables is composed of the sensitivities of its elementary rates. Each rate is weighted by the frequency of the initial state as well as by the reproductive value of the final state.

Now we turn our attention to determining the impact niche vectors. Here the starting point is: How does the change of the regulating variables receive contribution from the perturbation of the number of individuals in a given i -state of a given population? It is described by the $D \times s$ matrix \mathbf{F} via the relation

$$dI_m = \sum_{i=1}^L \sum_{j=1}^s F_{mj}^{(i)} dn_j^{(i)} \quad (m = 1, 2, \dots, D). \quad (3.8)$$

Matrix \mathbf{F} is considered to be directly calculable from the specific model.

In line with the definition of the impact niche vector, we want to express the perturbation $d\mathbf{I}$ solely by the total population sizes $d\tilde{n}^{(i)}$, as

$$dI_m = \sum_{i=1}^L C_m^{(i)} d\tilde{n}^{(i)} \quad (m = 1, 2, \dots, D). \quad (3.9)$$

Naively, one could expect that the vector

$$\tilde{C}_m^{(i)} = \sum_{j=1}^s F_{mj}^{(i)} p_j^{(i)} \quad (m = 1, 2, \dots, D) \quad (3.10)$$

plays the role of $\mathbf{C}^{(i)}$ (cf. Eq. (1.13)). Impacts of each state contribute to the impact of the population proportional to the frequency of that state. This would be the case if the population structures $\mathbf{p}^{(i)}$ were unperturbed. We will refer to $\tilde{\mathbf{C}}^{(i)}$ as the *uncorrected* impact vector of species i .

However, the equilibrium population structures receive perturbation also under the change of the dilution rates $\Delta^{(i)}$. As Appendix B demonstrates, the change of the equilibrium population structure \mathbf{p} is

$$dp_j^{(i)} = \sum_{k,l=1}^s A_{jk}^{(i)} dM_{kl}^{(i)} p_l^{(i)} \quad (j = 1, 2, \dots, s), \quad (3.11)$$

where

$$\mathbf{A}^{(i)} = \sum_{j \neq 1}^s \frac{(\mathbf{w}_j^{(i)} - U_j^{(i)} \mathbf{p}^{(i)}) \circ \mathbf{v}_j^{(i)}}{\rho_1^{(i)} - \rho_j^{(i)}} \quad (3.12)$$

is an $s \times s$ matrix describing the dependence of the population structure on the perturbations of the dynamical matrix. Matrix \mathbf{A} is finite provided that the dynamical matrix is primitive. The sum runs over the non-dominant eigenvalues/vectors, \circ denotes dyadic product and

$$U_j^{(i)} = \sum_{k=1}^s w_{jk}^{(i)} \quad (j = 2, \dots, s). \quad (3.13)$$

(Note that $U_1^{(i)} = 1$ by the normalization of w_1 . Similar normalization for $U_j^{(i)}$, $j \neq 1$ might not be possible, as these quantities are allowed to be zero.) Existence of $\mathbf{A}^{(i)}$ relies on the fact that the dominance of eigenvalue ρ_1 (cf. Appendix A) implies $\rho_1^{(i)} > \rho_j^{(i)}$ for all $j > 1$.

Combination of Eqs. (3.4) and (3.11) leads to

$$dp_j^{(i)} = - \sum_{k,l=1}^s \sum_{m=1}^D A_{jk}^{(i)} T_{klm}^{(i)} dI_m p_l^{(i)} \quad (j = 1, 2, \dots, s). \quad (3.14)$$

The perturbation of the population structure comes from the change of the total population size and from the change of the distribution. The total derivative of $n_j^{(i)} = \tilde{n}^{(i)} p_j^{(i)}$ gives

$$dn_j^{(i)} = d\tilde{n}^{(i)} p_j^{(i)} + \tilde{n}^{(i)} dp_j^{(i)} \quad (j = 1, 2, \dots, s). \quad (3.15)$$

From Eqs. (3.8), (3.14) and (3.15) we get

$$\sum_{n=1}^D (\delta_{mn} + H_{mn}) dI_n = \sum_{i=1}^L \sum_{j=1}^s d\tilde{n}^{(i)} F_{mj}^{(i)} p_j^{(i)} \quad (m = 1, 2, \dots, D), \quad (3.16)$$

where the $D \times D$ matrix \mathbf{H} is

$$H_{mn} = \sum_{i=1}^L \sum_{j,k,l=1}^s \tilde{n}^{(i)} F_{mj}^{(i)} A_{jk}^{(i)} T_{klm}^{(i)} p_l^{(i)} \quad (m, n = 1, 2, \dots, D). \quad (3.17)$$

It characterizes the consequences of the perturbed population structure on the regulation of the community. Note that matrix \mathbf{H} is a property of the ecosystem as a whole, therefore, it is the same for all species involved.

The impact niche vector is an immediate consequence of Eq. (3.16):

$$\mathbf{C}^{(i)} = \frac{\partial \mathbf{I}}{\partial n^{(i)}} = (\mathbf{1} + \mathbf{H})^{-1} \mathbf{F}^{(i)} \mathbf{p}^{(i)} = (\mathbf{1} + \mathbf{H})^{-1} \tilde{\mathbf{C}}^{(i)}. \quad (3.18)$$

Note that

$$\mathcal{V}_C = \frac{1}{\det(\mathbf{1} + \mathbf{H})} \mathcal{V}_{\tilde{\mathbf{C}}}. \quad (3.19)$$

Recall that matrix \mathbf{A} and therefore matrix \mathbf{H} is finite for primitive dynamical matrices. That is, the linear dissimilarity of the impact niche vectors is proportional

to the dissimilarity of the uncorrected impact vectors, with a nonzero constant of proportionality. The two impact niche vectors became linearly dependent under the same circumstances. Therefore, the empirically more accessible uncorrected vectors $\tilde{\mathbf{C}}^{(i)}$ could be a good proxy for the corrected ones.

Formulae (3.7) and (3.18) establishes the connection between the population-level niche vectors and the detailed (i-state-level) description of the structured population. With the exception of the correction represented by matrix \mathbf{H} , this relationships are intuitively transparent. The dimension reduction procedure depicted in Fig. 3.1 ensures that the calculated impact and sensitivity niche vectors obey the coexistence theory described above. Therefore, we succeeded in establishing the theory of limiting similarity and niche sensu Meszéna et al. (2006).

3.2 Spatial structure

The theory of Section 3.1 applies for any kind of structured populations with finite i-states. As the population structure may involve spatial structure also, spatiality is not a separate issue from a purely mathematical point of view. However, because of the ecological importance of spatial distribution, it worth considering the minimal model of spatiality, when the different locations are the only source of population structure as well as of species diversity. In this subsection we concentrate on the analytic consequences of these simplifications.

We assume that the investigated populations live in a metapopulation environment of s habitats, or patches, in which the environmental conditions may differ. The individuals are equivalent except their locations. Moreover, we assume that population regulation operates locally. In this case, the regulating variables (i.e. the resource exploitations) in the different patches must be considered as different variables (Levin, 1974), each of them has a contribution to the metapopulation-level regulation. There is a single and independent regulating variable in each patch ((Levene, 1953); “soft selection” regime (Christiansen, 1975)). As the total number of them is $D = s$, at most s species can coexist in a stable fixed point of the population dynamics.

The state transitions correspond to migration between habitats. They are specified by a migration matrix for each population. Its generic element $\mu_{jk}^{(i)}$ ($j, k =$

$1, 2, \dots, s$) represents the rate of migration of species i from patch k to patch j . Then the elements of the dynamical matrix are

$$m_{jk}^{(i)} = \begin{cases} r_j^{(i)} - \sum_{l=1}^s \mu_{lj}^{(i)} & \text{if } j = k \\ \mu_{jk}^{(i)} & \text{if } j \neq k \end{cases}. \quad (3.20)$$

It is assumed, that any patch is reachable from any other via consecutive migration steps. Irreducibility of the population matrix is ensured in this case. For simplicity we further assume that resource exploitation is proportional to the total number of individuals in the respective patch. Without losing generality, we choose the constant of proportionality to be 1. So, the regulating variable in habitat j is

$$I_j = \sum_i n_j^{(i)}, \quad (3.21)$$

where $n_j^{(i)}$ denotes the population size of species i in patch j .

The ecological tolerance of species i towards the environmental conditions of habitat j is described by the local intrinsic growth rate $r_{0j}^{(i)}$ in that patch. The actual local growth rate $r_j^{(i)}$ is assumed to be negatively affected by the resource exploitation I_j in patch j :

$$r_j^{(i)} = r_{0j}^{(i)} - \alpha I_j, \quad (3.22)$$

where α characterizes the strength of regulation.

The reduction of generality allows considerable simplification of the formulae developed in the previous section. The matrix $F^{(i)}$ (cf. Eq. (3.8)) becomes the identity matrix

$$F_{jk}^{(i)} = \delta_{jk}, \quad (3.23)$$

as a consequence of Eq. (3.21). Comparison of Eq. (3.20) with Eq. (3.22) shows that only the element M_{mm} of the dynamical matrix depends on the regulating variable I_m . Therefore,

$$T_{mnk}^{(i)} = -\alpha \delta_{mn} \delta_{nk}. \quad (3.24)$$

Then, Eq. (3.7) reduces to a simplified expression for the sensitivity niche vector:

$$\mathbf{S}^{(i)} = \alpha \begin{pmatrix} v_1^{(i)} p_1^{(i)} \\ v_2^{(i)} p_2^{(i)} \\ \vdots \\ v_s^{(i)} p_s^{(i)} \end{pmatrix}. \quad (3.25)$$

That is, the sensitivity towards the regulating factor in a given patch is the product of the local density and the reproductive value of the individuals in that locality. The growth rate of the population is more sensitive to the exploitation of that patches where a larger fraction of the population lives as well as to the ones where the possibilities to contribute to the next generations is better.

By Eqs. (3.10) and (3.23), the uncorrected impact vector is simply

$$\tilde{\mathbf{C}}^{(i)} = \mathbf{p}^{(i)}, \quad (3.26)$$

while the corrected one is

$$\mathbf{C}^{(i)} = (\mathbf{I} + \mathbf{H})^{-1} \mathbf{p}^{(i)} \quad (3.27)$$

from Eq. (3.18). That is, apart from the correction related to the perturbation of the population structure, the local impact of a population is proportional to ration of the population living in the given location.

Chapter 4

Model studies for heterogeneous environment

The chapter is based on the articles

A. Szilágyi, G. Meszéna: *Limiting similarity and niche theory for structured populations*. Journal of Theoretical Biology 258, 27-37 (2009)

and

A. Szilágyi, G. Meszéna: *Two-patch model of spatial niche segregation*. Evolutionary Ecology 23: 187-205 (2009)

4.1 Chain of habitats

This chapter shows the applicability of the niche theory of spatially structured environment introduced in the previous chapter. In Section 4.1.1 and 4.1.2 we define a model context as of a linear chain of habitats to show niche segregation along an environmental gradient and the connection between strength of the regulation and robustness of coexistence. In Section 4.2 we restrict our attention to a two patch model as the minimal model of heterogeneous environment. We analyzed analytically this simplified context from both ecological and evolutionary point of view.

4.1.1 Model definition and methods

Here we define a spatial model for numerical investigations. We assume a linearly ordered chain of patches. Migration is possible between the neighboring habitats (Fig. 4.1). The migration rate from patch j to patch $j \pm 1$ is $\mu_{j\pm 1,j}$ uniformly for all species (Fig. 4.1). Then the dynamical matrix is

$$\mathbf{M}^{(i)} = \begin{pmatrix} r_1^{(i)} - \mu_{12} & \mu_{21} & \dots & 0 \\ \mu_{12} & r_2^{(i)} - \mu_{21} - \mu_{23} & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \mu_{s-1,s} & r_s^{(i)} - \mu_{s-1,s} \end{pmatrix}. \quad (4.1)$$

If all the μ 's are nonzero, the matrix $\mathbf{M}^{(i)}$ is irreducible, as required.

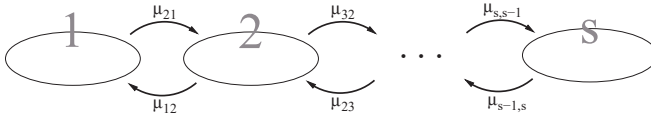


Figure 4.1: Chain of several habitats, migration is allowed between the nearest neighbors.

The 4th order Runge-Kutta method was used to study the dynamics (3.1). The equilibrium densities were determined by numerical integration until convergence. We have never found an internal attractor other than the unique fixed point. (This

is the main advantage of using continuous time.) As a consequence, at most so many populations can coexist, as many patches we consider.

At the equilibrium point, each eigenvalue and the corresponding left and right eigenvectors of the dynamical matrix for all populations were determined numerically. Then, the theory of Section 3.2 provided the impact and sensitivity niche vectors of the coexisting species. Finally, the regulation strength J of the community was calculated via Eqs. (2.15) and (2.17).

The theoretical prediction about the robustness of coexistence, provided by the regulation strength, was compared to the numerically determined robustness. To this end, the equilibrium was studied as a function of the extra mortalities with the constraint

$$\sum_{i=1}^L \Delta^{(i)} = 0. \quad (4.2)$$

That is, the perturbations affecting all populations identically (i.e., not introducing advantage/disadvantage) were disregarded. The combination of the $\Delta^{(1)}, \Delta^{(2)}, \dots, \Delta^{(L)}$ values, that allows coexistence, fills an $L - 1$ dimensional volume (the coexistence volume), which is the subset of the simplex defined by Eq. (4.2). The volume of the simplex is proportional to the robustness of coexistence.

4.1.2 Analysis of the system

We assume that the environmental conditions change monotonically along the chain of s habitats. Coexistence of $L = s$ species will be investigated. Species i is optimized to the conditions in patch i . We specify the intrinsic local growth rate of species i in patch j as a Gaussian function

$$r_{0j}^{(i)} = \frac{A}{\sqrt{2\pi}\sigma} e^{-\frac{(i-j)^2}{2\sigma^2}}, \quad (4.3)$$

where A is a scale-factor.

As an additional complication, we introduce an asymmetry to migration. Imagine, for instance, migration of flying insects in an environment with a dominant wind direction from the left to the right. While all migration rates to the right are higher,

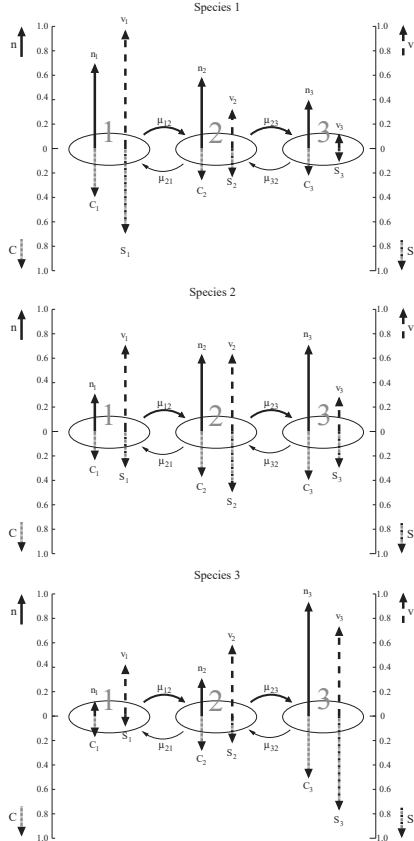


Figure 4.2: Coexistence of three species in three patches with asymmetric migration. Each pane represents one of the species. In each patch the lengths of the two upward-pointing arrows represent the population size and the reproductive value of the species in the given patch. Similarly, downward-pointing arrows represent the impact and sensitivity of the population towards the specific patch. Parameters: $A = 1/40$; $\sigma = 1$; $\alpha = 10^{-3}$; $\mu = 0.05$; $c = 1.5$.

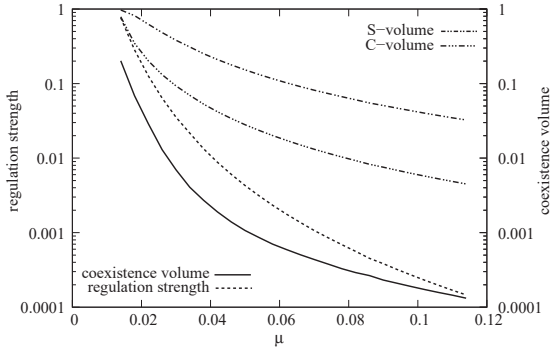


Figure 4.3: Determinant J and the regulating volume as a function of the migration rate μ . An arbitrary scaling was applied on the volume curve. The average and the maximal volumes are the same with the precision of line thickness. The other parameters are the same, as in Fig. 4.2.

the ones to the left are lower than a reference rate μ by a factor of c ($\mu_{j;j+1} = c\mu$ and $\mu_{j+1;j} = \mu/c$ for $j = 1, \dots, s-1$).

Fig. 4.2 depicts the population and niche vectors for $s = 3$. According to (4.3) Species 1, 2 and 3 have the highest fitness in Patch 1, 2 and 3, respectively. The migration difference between the two directions redistribute the *density* compared to the symmetric migration. This asymmetry in migration makes the differences of density between the patches smaller for Species 1 and larger for Species 3 than in the symmetric migration case.

The *reproductive value* of Species 1 decreases monotonically and rapidly in the direction of large migration. For Species 3, it changes in the opposite way, but this change is less pronounced. The reason is that an individual of Species 3 in Patch 2, or in Patch 1 has a high chance to move into a better patch. So, the reproductive value of an individual in a suboptimal patch has a higher reproductive value than without the asymmetric migration. For Species 2, there is only a small difference between the reproductive values in patch 1 (from where the migration take individuals to the optimal patch) and in patch 2 (which is the optimal patch itself).

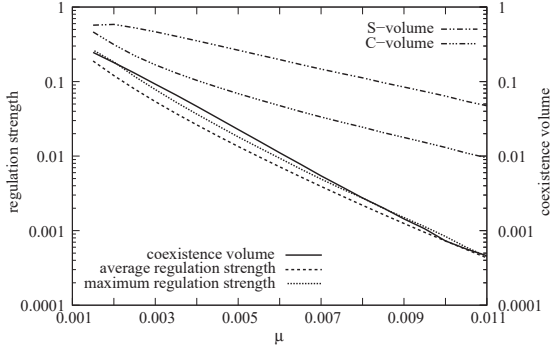


Figure 4.4: The same analysis, as in Fig. 4.3, for five patches. Parameters are unchanged except $\sigma = 1/2$.

As one expects, a species is most sensitive and has the highest *sensitivity* in its own optimal patch. Recall, that sensitivity is the product of the frequency and the reproductive value. For Species 1 and 3 both of these quantities have a clear maximum in their respective optimal patch. For Species 2 the two quantities changes from patch to patch in the opposite way. Consequently, the sensitivity values of Species 2 are more even across the metapopulation, a kind of more 'generalist' behavior.

Figs. 4.3 and 4.4 present the result of the robustness analysis for $s = 3$ and for $s = 5$, respectively. The coexistence volume is plotted as a function of the migration rate. The volume spanned by the impact vectors as the volume of the sensitivity vectors and the regulation strength $J = \det(a)$ are plotted also as a function of the migration rate. In our simple case $L = s$ then the regulation strength is simply the product of the two volumes $J = \mathcal{V}_C \cdot \mathcal{V}_S$. (Both of the average and the maximum of J over the coexistence volume were determined and plotted, where different.) For $s = 3$, the coexistence volume was determined via systematic screening of the simplex. In case of more patches and species this procedure would require immense computation. Instead, the more efficient Monte-Carlo integration was applied for $s = 5$. That is, we tested coexistence at a large number of randomly chosen points of the simplex. Measuring the probability of coexistence under uniform distribution

of the extra mortalities provided the coexistence volume. Increased migration tends to equalize the distribution of each population along the chain. This, in turn, makes the impact, as well as the sensitivity niches of the species more similar, resulting in a decreasing strength of regulation. This tendency predicts less robust coexistence for increasing migration rate. It is confirmed by the also decreasing coexistence volume. Note the quite parallel decrease of the two (independently calculated) quantities by more than two orders of magnitude during a ten-fold increase of the migration rate. While not plotted, the coexistence volume shrinks roughly isotropically. That is, we found no direction of perturbation for which the coexistence is extremely sensitive, as compared to the other directions.

4.2 Two patch environment

4.2.1 Model definition

For analytical tractability we restrict our attention to a “minimal model” of environmental heterogeneity. As a simplification of the previously introduced model and following Meszéna et al. (1997), we consider an environment consisting of two habitats of equal size, A and B , with different environmental conditions. As the number of regulating factors is $D = 2$, at most two species can coexist in equilibrium.

We assume a symmetric migration rate μ between patch A and B for all species. The population dynamics is defined as (cf. Eq. (4.1))

$$\frac{d}{dt} \begin{pmatrix} n_A^{(i)} \\ n_B^{(i)} \end{pmatrix} = \begin{pmatrix} r_A^{(i)} - \mu & \mu \\ \mu & r_B^{(i)} - \mu \end{pmatrix} \begin{pmatrix} n_A^{(i)} \\ n_B^{(i)} \end{pmatrix} \quad (4.4)$$

for all i , where

$$r_j^{(i)} = r_{0j}^{(i)} - \alpha I_j \quad (4.5)$$

is the actual growth rate as in Eq. (3.22). The local intrinsic growth rate $r_{0j}^{(i)}$ of species i in patch j is a fixed property and in this section do not follow Eq. (4.3). The overall growth rate of the population and the dynamics of spatial relaxation at fixed values of the regulating variables can be calculated from the eigenvalues of this matrix, cf. Section 1.1, see Box 4.1.

The niche vectors were calculated in two ways with coinciding results. First, they were calculated from the numerically determined equilibrium distribution by

Box 4.1: Population growth and relaxation in the model

Following the lead of Metz and Diekmann (1986), Diekmann et al. (1998, 2001, 2003) consider first the dynamics of a population at fixed I . This condition means that the loop of population regulation is cut open, the populations become independent and grow exponentially after an initial spatial relaxation.

The relevant quantities are the two eigenvalues of the dynamical matrix:

$$\rho^{(i)\pm} = \frac{r_A^{(i)} + r_B^{(i)}}{2} - \mu \pm \sqrt{\left(\frac{r_A^{(i)} - r_B^{(i)}}{2}\right)^2 + \mu^2}. \quad (4.6)$$

The exponential growth rate, that plays the role of overall growth rate $r^{(i)}$ in the general setup, is the leading eigenvalue, i.e., $r^{(i)} = \rho^{(i)+}$. It is instructive to calculate two limiting cases:

$$r^{(i)} \approx \begin{cases} (r_A^{(i)} + r_B^{(i)})/2 & \text{if } \mu \gg |r_A^{(i)} - r_B^{(i)}|/2, \\ \max(r_A^{(i)}, r_B^{(i)}) - \mu & \text{if } \mu \ll |r_A^{(i)} - r_B^{(i)}|/2. \end{cases} \quad (4.7)$$

While the overall growth rate is the average of the local growth rates when the migration is high, it roughly equates to the higher local growth rate when the migration is low.

the analytic formulae of Box 4.2 (see Appendix C). Second, they were determined via numerically reproducing the thought experiment described at the end of Section 3.1, see p. 36.

4.2.2 Fundamental niche of a single species and niche segregation between two species

Behavior of the population is characterized by four two-dimensional vectors; the two dimensions correspond to the two habitats:

Box 4.1 (cont.)

The equilibrium distribution is given by the eigenvector of the dynamical matrix. It is easy to see, that an additional mortality, which is the same in the two patches, does not alter this distribution. The rate of relaxation to the equilibrium distribution is determined by the difference between the two eigenvalues:

$$\Delta\rho^{(i)} = \rho^{(i)+} - \rho^{(i)-} = \sqrt{\left(r_A^{(i)} - r_B^{(i)}\right)^2 + 4\mu^2}. \quad (4.8)$$

Observe that there are two processes contributing to this relaxation. The first one is the difference between the local growth rates. It tends to redistribute the population into the patch that is better for the species. Another one is the migration that tends to equalize the distribution between the patches. When $r_A^{(i)} - r_B^{(i)} = \mu = 0$, there is no relaxation, i.e., the initial distribution is retained.

Consider now the realistic case, when the regulation loop is closed. Then, the regulating variables are adjusted until the equilibrium condition $r^{(i)} = \rho^{(i)+} = 0$ is met. An additional mortality may change the equilibrium distribution through modifying the equilibrium \mathbf{I} . This effect becomes stronger, when the \mathbf{I} -independent relaxation is weak, i.e., when $\Delta\rho^{(i)}$ is small.

- The vector $\mathbf{r}_0^{(i)} = (r_{0A}^{(i)}, r_{0B}^{(i)})$ of tolerances.
- The vector $\mathbf{n}^{(i)} = (n_A^{(i)}, n_B^{(i)})$ of abundances.
- The impact niche vector $\mathbf{C}^{(i)} = (C_A^{(i)}, C_B^{(i)})$.
- The sensitivity niche vector $\mathbf{S}^{(i)} = (S_A^{(i)}, S_B^{(i)})$.

$\mathbf{r}_0^{(i)}$ is a fixed property of the species. Its *direction* represents the *relative* tolerance with respect to the patches. A change of the *length* of $\mathbf{r}_0^{(i)}$ would correspond to an increase/decrease of the fitness of the species. We will chose all tolerance vectors to have the same length, because the fitness differences will be

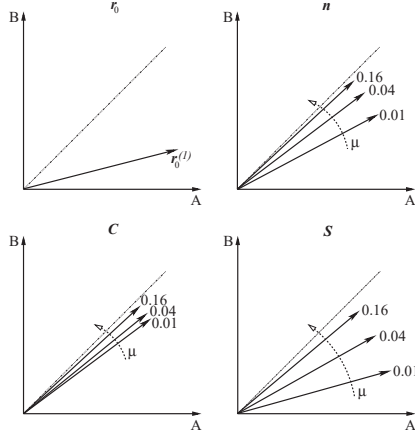


Figure 4.5: The four two-dimensional vectors, describing a lone population, at different values of the migration rate μ . The tolerance vector $\mathbf{r}_0^{(1)} = (0.04, 0.01)$ is a fixed property of the species, independent of μ . The angle between this vector and the 45° direction is a measure of specialization. The vector $\mathbf{n} = (n_A, n_B)$ of abundances approaches the 45° direction – representing the even distribution – with increasing migration. The impact niche \mathbf{C} and the sensitivity niche \mathbf{S} behaves similarly. ($\alpha = 0.008$ and $A = 1$ is used here and for the other figures.)

scaled via the (possibly negative) extra mortality $\Delta^{(i)}$. Note, that it is a matter of definition, which mortality is considered as “extra”. Accordingly, $\Delta^{(i)} = 0$ means nothing else here, than correspondence to the arbitrary choice of having tolerance vectors of equal lengths.

The vectors $\mathbf{n}^{(i)}$, $\mathbf{C}^{(i)}$ and $\mathbf{S}^{(i)}$ of a species are determined together by its tolerance vector, the migration rate and the possible competition between the species. Fig. 4.5 shows the behavior of the four vectors for a single species at different migration rates. Fig. 4.6 demonstrates the effect of competition, i.e., the comparison between the behaviors of two species, when alone, and when together. Fig. 4.7 depicts the detailed dependence on the migration rate in a different representation: the angle

Box 4.2: Niche vectors of the model

We provide analytic formulae for the niche vectors; see the Appendix C for the derivations. For the i th species, the sensitivity niche is determined by the distribution of the species between the patches:

$$\mathbf{S}^{(i)} = \frac{\alpha}{\left[\left(n_A^{(i)} \right)^2 + \left(n_B^{(i)} \right)^2 \right]} \begin{pmatrix} \left(n_A^{(i)} \right)^2 \\ \left(n_B^{(i)} \right)^2 \end{pmatrix}. \quad (4.9)$$

The sensitivities are proportional to the *square* of the local densities by the following reason. *First*, the larger is the fraction of the population living in one of the patches, the more sensitive its overall growth rate is to the resource exploitation in that patch. This effect alone would lead to a simple proportionality. *Second*, the individuals themselves have different possibilities to contribute to the future generations depending on the quality of their patch. The latter effect is described by the notion of the “reproductive value” of the individual in the given patch. The reproductive values are elements of the left eigenvector of the dynamical matrix, while the equilibrium distribution corresponds to the right eigenvector (see Section 1.1.2). As our dynamical matrix happens to be symmetric, the left and the right eigenvectors are the same. That is, the reproductive value in a patch is proportional to the population density in that patch, leading to the quadratic dependence of the sensitivity.

between the respective vector and the A axis is plotted. Figs. 4.8 and 4.9 present the results on the robustness of coexistence.

Hutchinson (1978) distinction between the fundamental and the realized niches is implemented by calculating the niche of a species in absence, and in presence, of its competitors, respectively (Meszéna et al., 2006). Here we study the (fundamental) niche of a lone species; the (realized) niches of coexisting species will be considered in the next section.

Box 4.2: (cont)

The impact niche is

$$\mathbf{C}^{(i)} = \frac{1}{2G+1} \left[\frac{1}{n_A^{(i)} + n_B^{(i)}} \begin{pmatrix} n_A^{(i)} \\ n_B^{(i)} \end{pmatrix} + G \begin{pmatrix} 1 \\ 1 \end{pmatrix} \right], \quad (4.10)$$

where

$$G = \sum_i \frac{\alpha}{\Delta\rho^{(i)}} \frac{n_A^{(i)} n_B^{(i)}}{n_A^{(i)} + n_B^{(i)}}. \quad (4.11)$$

The first term is easy to interpret: the impact of a population on one of the patches is proportional to its relative abundance in that patch. The second term is a consequence of the fact that the population distribution changes with perturbation. The second term is large, when the small $\Delta\rho^{(i)}$ s make the change of the distribution significant (Box 4.1). In case of $\mu = 0$, the local growth rates are regulated to zero independently (i.e., $r_A^{(i)} = r_B^{(i)} = 0$), implying $\Delta\rho^{(i)} = 0$. Then the second terms dominates $\mathbf{C}^{(i)}$, that has direction 45° .

The abundance vector \mathbf{n} of our species behaves as it is expected intuitively. At very low migration rates, the population lives predominantly, but not exclusively, in the patch that is better for it. Increasing migration rate tends to equalize the local abundances. That is, the angle of vector \mathbf{n} converges to 45° with increasing migration rate (Fig. 4.5; Fig. 4.7 top row, continuous curve).

The sensitivity niche vector \mathbf{S} behaves similarly. The population, as a whole, is more sensitive to the patch that is more suitable for it. This effect is actually a double one. The inferior patch contains a smaller fraction of the population *and* any specific individual in that patch has a disadvantage in contributing to the future generations (Box 4.2). Therefore, the difference between the sensitivities in the two patches is more pronounced than between the densities. As plotted in Fig. 4.7 (top row, dotted curve), the sensitivity niche vector lies farther apart from the 45° direction, than the abundance vector. Still, the two vectors share the property of converging to the 45° direction for large migration rate.

The impact niche vector \mathbf{C} is a sum of two vectors. One of them is proportional to the abundance vector, while the other one has a 45° direction (Box 4.2). (The latter component is the consequence of the fact that the equilibrium population distribution changes also as a consequence of the perturbation of the total population size.) Therefore, vector \mathbf{C} lies in between vector \mathbf{n} and the 45° direction (Fig. 4.5; Fig. 4.7, top row, dash-dotted curve). Direction of vector \mathbf{C} changes non-monotonously with migration rate (Fig. 4.7).

At $\mu = 0$, \mathbf{C} lies exactly in the 45° direction. In this case the subpopulations in the two patches are regulated separately. An additional mortality decreases the two local densities with the same *amount*, instead of by the same *ratio*. With slightly increased migration rate, the direction of \mathbf{C} approaches the direction of \mathbf{n} . Then, at high migration rate, \mathbf{n} and \mathbf{C} converges to the 45° direction together.

Consider now coexistence of two species. Fig. 4.6 demonstrates the effect of competition on the vectors \mathbf{n} , \mathbf{C} and \mathbf{S} . One can observe that the spatial distributions of the coexisting species are more segregated than their distributions, when alone. The same applies to the $\mathbf{C}^{(i)}$ s and the $\mathbf{S}^{(i)}$ s, as the niche vectors are related to the abundance vector (Box 4.2). Using the term of Hutchinson (1978), the realized niches are more segregated than the fundamental ones.

Fig. 4.7 depicts the same comparison as a function of the migration rate. Without migration, the “coexisting” Species 1 and 2 are completely segregated into patches A and B, respectively. Their impact and sensitivity niches behave accordingly. This remains true even if one considers competition of the specialist Species 2 with a generalist one denoted by G .

While the two patches are equally appropriate for the generalist without competition, it is restricted to patch A when patch B is occupied by the specialist.

In particular, note that the angle of the impact vectors of the two coexisting species are 0° and 90° (i.e., the segregation of the impact niches are complete) for $\mu = 0$, *despite* the fact that both of the fundamental impact niches have the angle 45° . Complete segregation at zero migration rate implies, that weak enough migration results in wide segregation of the realized niches even if the difference in the tolerance vectors (consequently: the difference in the fundamental niches) are not so large. That is, a relatively low physiological difference may be sufficient for robust coexistence provided that the migration is weak.

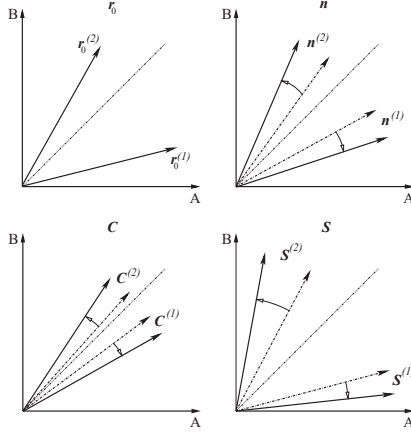


Figure 4.6: *Effect of competition on two coexisting species, which are characterized by the tolerance vectors $\mathbf{r}_0^{(1)} = (0.04, 0.01)$ (the same as in Fig. 4.5) and $\mathbf{r}_0^{(2)} = (0.02, 0.036)$. In the \mathbf{n} , \mathbf{C} and \mathbf{S} plots, the dashed and solid arrows represents the populations, when alone, and while they coexist, respectively. Competition makes the population distributions and the niches more segregated. ($\mu = 0.01$ is used.)*

Like in the one-species case, the increasing migration makes the distributions more even, i.e., the angle of the vectors $\mathbf{n}^{(i)}$, as well as the niche vectors, approach the 45° . That is, the segregation of the fundamental, as well as of the realized, niche diminishes with increasing migration even if the difference in the tolerance vectors is significant.

These results indicate that dissimilarity of the tolerance vectors and the migration rate are the two relevant variables that determine the segregation of the realized niches. We demonstrate the connection between the robustness of coexistence and the niche dissimilarity in both respects.

Fig. 4.8 presents dependence on the angle between the two tolerance vectors at a given value of the migration rate. The non-surprising observation is, that the dissimilarity of the abundance vectors, as well as the dissimilarity of both kinds of niche vectors go to zero together with the dissimilarity of the tolerance vectors. The

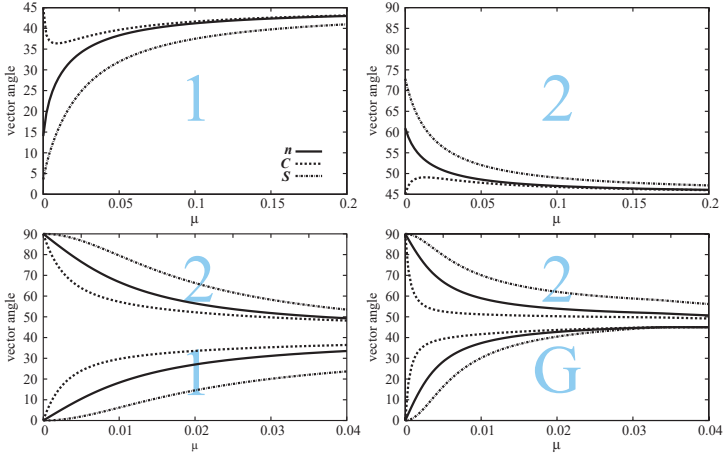


Figure 4.7: The angle of vectors \mathbf{n} , \mathbf{C} and \mathbf{S} with respect to axis A , as a function of the migration rate. The two specialist species (denoted by “1” and “2”) are characterized by the tolerance vectors that were used already in Fig. 4.6. The generalist Species “G” has the uniform tolerance $\mathbf{r}_0^{(G)} = (0.029, 0.029)$. The two upper plots represent the specialists, when alone. The lower plots depict coexistence of Species 2 with Species 1 (lower left) and with Species G (lower right). Again, coexistence makes the populations more segregated. At extremely low migration, they are separated completely.

significant point is that the region of the extra mortality, that allows coexistence, shrinks to nil also.

If the tolerance vectors of the two species coincide, the (neutral) coexistence requires exact equality of the fitness; an arbitrarily small extra mortality is detrimental for the coalition. At small difference between the tolerances, a small difference in the fitness is allowed. Robust coexistence, that is not very sensitive to external perturbations, requires significant difference in the tolerances.

Fig. 4.9 depicts the dependence on the migration rate. In this specific example, at $\Delta^{(1)} = 0$, the first species dies out when the migration rate becomes larger than

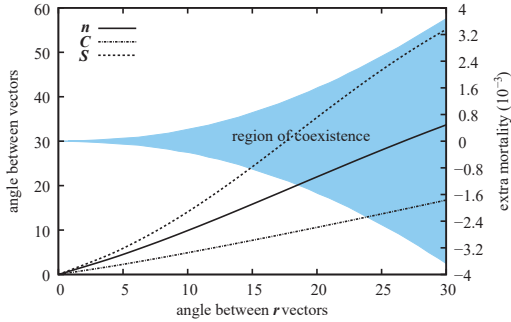


Figure 4.8: *Robustness of coexistence of two species against an extra mortality $\Delta^{(1)}$ of the first species is plotted as a function of the angle between the two tolerance vectors. Species 1 is characterized again by the tolerance vector $\mathbf{r}_0^{(1)} = (0.04, 0.01)$. The tolerance vector of Species 2 is specified via the angle between the two vectors. The gray region represents the interval of the extra mortality, which allows coexistence, as a function of the migration rate. The curves depict the angle difference between the two \mathbf{n} vectors, the two \mathbf{C} s and the two \mathbf{S} s. Observe the correlated changes: As the direction of the tolerance vectors become more similar, so do the niches of the two species. Accordingly, the region of coexistence shrinks. ($\mu = 0.01$ is used.)*

a given value. However, this threshold is not a strict upper bound on migration, or on niche similarity, that constrains coexistence. Species 1 dies out because it is more specialized, than Species 2, so it is affected adversely by increased migration. If this negative effect is compensated by a fitness advantage represented by a negative $\Delta^{(1)}$, coexistence is still possible, and remains possible even at high migration rates.

Nevertheless, this additional gain in fitness should not be too large, because Species 2 will be outcompeted then. At large migration rate, only a small range of $\Delta^{(1)}$ allows coexistence. Like increasing similarity of the tolerances, increasing migration decreases niche-segregation, therefore it is detrimental to coexistence. Note that our Figs. 4.8 and 4.9 are in complete analogy with Fig. 6.4 of May (1973, p. 158).

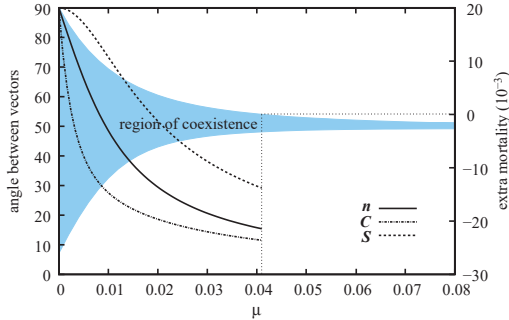


Figure 4.9: Robustness of coexistence of the two species of Fig. 4.6 against an extra mortality $\Delta^{(1)}$ of the first species is plotted as a function of migration rate. Notations are the same as in Fig. 4.8. Robustness decreases with increasing migration, as the niches become similar. Increasing migration is more advantageous to the more generalist type, so the more specialized Species 1 dies out at $\mu = 0.041$. At larger migration rate, coexistence is possible only for negative $\Delta^{(1)}$. The allowed $\Delta^{(1)}$ interval is getting narrower with increase of μ . (The curves are calculated for $\Delta^{(1)} = 0$, so they are not continued after $\mu = 0.041$.)

4.2.3 Evolving tolerances

Now we turn our attention to the adaptive dynamics of the model following (Mesz na et al., 1997). The relevant evolutionary question is whether a single strategy, a “generalist”, or a pair of specialists will exploit the two patches.

In this evolutionary study we assume that a species’ tolerances are determined by an evolvable trait, or strategy, x . The trait have different optima, denoted by x_A^{opt} and x_B^{opt} in the two patches. Then, the local intrinsic growth rate of strategy x in patch $j = A, B$ is specified as

$$r_{0j}(x) = \frac{A}{\sqrt{2\pi}\sigma} e^{-\frac{(x-x_j^{\text{opt}})^2}{2\sigma^2}}. \quad (4.12)$$

In line with the methodology of adaptive dynamics (Metz et al., 1996; Mesz na et al., 1997; Geritz et al., 1997, 1998), the strategy is clonally inherited. Populations of the existing strategies follow the dynamics (4.4). Occasionally, a mutant strat-

egy, that is similar to an already existing one, appears with a low population size. Strategies reaching an extremely low populations size are considered extinct.

We choose $\sigma = 1$ and $A = 1$ in Eq. (4.12) as a fixation of the scale and specify that

$$x_A = \frac{d}{2} \quad \text{and} \quad x_B = -\frac{d}{2}, \quad (4.13)$$

where $d = x_A - x_B$ is the difference between the two optima. Note that $x = 0$ is the “central” strategy that implement the compromise between the two patches. We have two free parameters to specify the evolutionary problem: the patch difference d and the migration rate μ . The fitness of a strategy can be defined as its exponential growth rate r , as calculated in Box 4.1 (Metz et al., 1992).

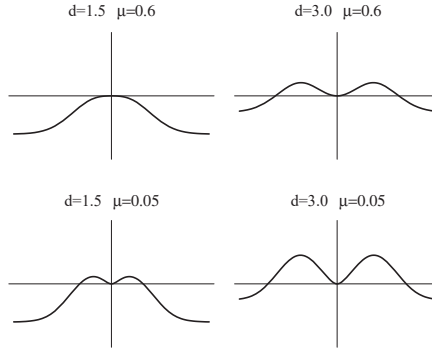


Figure 4.10: *Invasion fitness function for four combination of the patch difference d and migration rate μ in the evolutionary version of the model. Horizontal axes: strategy; vertical axes: fitness. It is assumed that the two patches are loaded symmetrically. This happens, for instance, if the central strategy is the only one present. The central strategy is a local maximum (an ESS) if the patch difference d is sufficiently small and the migration rate μ is sufficiently large. In the rest of the cases, when either the migration rate decreases sufficiently, or the patch difference increases sufficiently, the central strategy becomes a pessimum between two – more specialized – optima.*

It is instructive to consider first the symmetric situation, when the two patches are equally exploited: $I_A = I_B$ (Fig. 4.10). This happens if either the central strategy is present alone, or two symmetrically located strategies exist in equal size. According to Box 4.1, in the case of large migration rate the fitness function is a *sum* of two Gaussian functions, with distance d between their peaks. This sum is unimodal for a small d , but bimodal for a large one. On the other hand, if μ is small, the fitness is the *maximum* of the two exponentials. Such a function is always bimodal. That is, in the symmetric case, the fitness function is unimodal with a fitness maximum at the central strategy for large μ and small d . Either decreasing migration or increasing patch difference lead to bimodal fitness function with a minimum at the central strategy.

This analysis specifies the evolutionary stability of the central strategy. It is an ESS if and only if the patch difference is small enough and the migration rate is large enough. This result is in agreement with the common sense, as well as with the niche analysis of the previous sections: significant patch difference and low migration make specialization to one of the patches possible.

Asymmetric loading of the patches by a specialized strategy introduces negative frequency dependence, as adaptation to the overloaded patch becomes less favored. The possible consequence is that evolution may converge first to the central strategy, even if it is not an ESS. Then, evolutionary branching happens, and two specialist strategies appear. The phase portrait in the leftmost pane of Fig. 4.11 depicts the stability of the central strategy as a function of the parameters. First, decreasing migration and/or increasing patch difference changes this strategy from an ESS to a branching point. Further parameter change, however, makes the central strategy so disadvantageous, that it becomes an evolutionary repeller.

The more complete evolutionary behavior of the model is represented on the remaining two panes of Fig. 4.11. When the generalist strategy is a repeller, then evolution converges to a more specialized strategy and may, or may not branches there. Evolutionarily stable coexistence of two specialists may be possible even if it is evolutionarily unreachable from a monomorphic case. See (Meszéna et al., 1997) for further details.

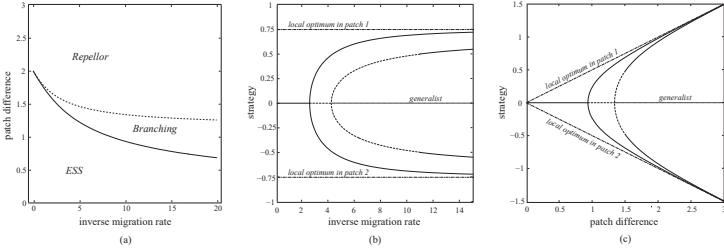


Figure 4.11: *Behavior of the evolutionary model. (a) Phase portrait of the stability of the central strategy as a function of parameters: the patch difference d and the inverse migration rate $1/\mu$. The other two panes depict the complete behavior as a function of the inverse migration rate at fixed $d = 1.5$ (b) and as a function of the patch difference with fixed $\mu = 0.1$ (c). In (b) and (c), vertical axis is the strategy. The dotted-dashed lines at $x = \pm d/2$ represent the local optima in the patches. All other lines represent singular strategies. Thin lines: monomorphic singular strategies; thick line: dimorphic singular strategy. Continuous lines: ESS; dashed: branching strategy; dotted: repellor.*

4.3 Discussion

Competitive exclusion and limiting similarity are unavoidable concepts of evolutionary ecology. Here we contributed to their theory by extending the analysis of Meszena et al. (2006) for structured populations. By studying coexistence of spatially structured populations we established the mathematical meaning of spatial niche segregation. Instead of using the phenomenological concept of resource utilization, the background theory of Meszena et al. (2006) describes the niche of a species by the population’s impact on, and sensitivity towards, the regulating variables. We developed the connection between the population-level niche-description and the impact/sensitivity of the individual states. It was found that population distribution is an acceptable proxy for these quantities.

We stress the generality of our approach. Limiting similarity was proposed in the context of the competitive Lotka–Volterra model (MacArthur and Levins, 1967). Being a “strategic” model, it maintains little connection with the complications of

most of the ecological situations. However, expecting and not finding a strict limit of similarity in other model studies caused disillusionment towards limiting similarity (Maynard Smith and Szathmáry, 1995; Rosenzweig, 1995). Only a model-independent analysis can provide a firm answer to the question whether limiting similarity and niche theory are proper guides of biological thought.

One source of our generality is the perturbation approach. Instead of searching for a strict limit of similarity, we studied the gradual loss of robustness with increasing similarity. This change of attitude was suggested first by Abrams (1983) (“similarity–coexistence relationship”, see also May, 1973, p. 158); a model-independent analysis was provided by Meszén et al. (2006). We tested robustness of coexistence via varying the extra mortalities $\Delta^{(i)}$.

Another source of generality is the notion of regulating variables. Levin (1970) demonstrated already that the (discrete) principle of competitive exclusion (MacArthur and Levins, 1964; Rescigno and Richardson, 1965) can be generalized beyond resource competition by counting all quantities that behaves like a resource concentration (see also Heino et al., 1997). Unfortunately, the unifying nature of this idea did not receive the proper attention in community ecology. Instead, a multitude of reasons, which invalidates the resource competition theory, was investigated (e.g. Schoener, 1976). Following Krebs (2001), we prefer to use the term “regulating variables” for all variables included in the regulating feedback loop, because “limiting factors” often means external ecological conditions, like temperatures, that are not density-dependent and, therefore, not regulating. It is essential that *all* interactions between the individuals must be considered as mediated by the regulating variables.

As competitive exclusion is avoided by diversification with respect to the regulating variables, the *set* of these variables is the proper generalization of Hutchinson’s “niche space” (Meszén et al., 2006). This “space” is either a discrete set, when we are dealing with a finite number of regulating variables, or a continuous entity, spanned by the “niche axes”. The canonical example for the latter case is the seed-size continuum, partitioned by consumer populations. Importantly, the niche axis is the seed-size and *not* the seed densities. The latter ones are the (infinitely many) regulating variables.

The “Eltonian” and the “Grinnellian” niches (or profession and address niches, see Section 1.2.2) are often perceived as very different (Leibold, 1995). The first

one describes the function of the species within a given habitat, while the second one characterizes the allowable habitat for a species of a given function (cf. the “bionomic” and “scenopoetic” niche axes of Hutchinson, 1978 for the continuous case). Again, the notion of regulating variables plays the role of the unifying concept. As pointed out by Levin (1974), the concentrations of a given kind of resource in the different habitats are different variables in the feedback loop. Therefore they should be counted, as different regulating variables, just like if they were functionally different regulators within a single habitat. This way, both kinds of niche-segregation can be considered as segregation with respect to the regulating variables.

Still, the description of habitat-segregation is more complicated than the functional one because it must involve handling the spatial structure of the populations. This problem was solved here together with any other kinds of population structure. See also Szabó and Meszéna (2007) for a different study that emphasizes the role of localized vs. non-localized regulation in coexistence.

When the nature of the niche space is understood, the next issue is the specification of the niche of a given species within that space. Originally, species’ niche was conceived as a subset (Hutchinson, 1957) of the niche space. Later, it was made more precise by introducing the resource utilization function (MacArthur and Levins, 1967), describing the “fuzzy” nature of the subset. Unfortunately, this function is entirely a phenomenological concept, for which no unequivocal measuring instruction exists. Operationally, one has to study two questions, instead of one (cf. Abrams, 1988; Goldberg, 1990): How does resource availability depend on the population density? How does population growth rate depend on resource availability? The niche theoretical relevance of the two-way interaction was recognized by Leibold (1995). Meszéna et al. (2006) introduced the differential measures of these relations, the impact and the sensitivity vectors, as the proper representation that connects niche segregation and coexistence in a precise and general way.

Here we provided the exact connection between the population-level sensitivity niche vector and the sensitivity of the elementary demographic rates. Let us phrase it for age structure and discrete time! The sensitivity of the survival rate from age 4 to age 5 contributes to the population-level sensitivity proportional to the fraction of individuals in the age-class 4 in the equilibrium age-distribution *and* by the reproductive value of an individual of age 5. The reproductive rate in age 4

contributes according to the frequency of the 4-years-olds and to the reproductive value of a newborn. The very same intuitive idea applies for any other types of population structure. (This result was a direct application of the sensitivity analysis by Caswell, 2001). In our spatial examples the *i*-state sensitivity was the same in each habitat. Then the population sensitivity towards the regulating factor in a given patch was just determined by the local density and reproductive value. In case of symmetric migration this dependence reduces to square local density (cf. Eq. (3.25) and Box 4.2).

The impact case is more involved. One must not consider the state distribution as a fixed property of the population. As the different states may be regulated differently, the population structure may become perturbed under a change of the population size. Moreover, the structures of the coexisting populations mutually influence each other through competition. An extra mortality of one of the species may perturb the state-distribution of all of them. To be precise, one must take into account all of these interrelated structure-perturbations when the environmental impact of a change in a population size is calculated. This is the role of matrix \mathbf{H} in Eq. (3.18).

Empirical determination of the matrix \mathbf{H} would be an immense task. Fortunately, for the qualitative limiting similarity conclusion it is sufficient to consider only the uncorrected version of the impact niche vectors (cf. Eq. (3.19)). It is just the sum of the impacts of all states, weighted by the frequencies of the states (Eq. (3.10)). No precision is lost this way. The true impact niche vectors, corrected by using matrix \mathbf{H} , were needed only to calculate the community matrix (2.15). Fortunately, it is possible to determine in a more direct way through Eq. (2.20) via experimentally applied extra mortality. Still, the consistency of niche theory requires us to state clearly that the corrected impact vector plays the prescribed role for structured populations.

It is quite common, but not necessary, that individuals in different *i*-states, like the larval and the adult stages of an insect, consume different resources. Our theory provides a clear prescription for constructing the niche description of the insect population from the ones for the larva and for the imago. In general, the number of regulating factors and the number of the *i*-states are unrelated. Nevertheless, in the spatial examples we considered, there was a single resource in each patch, leading to $s = D$.

Without a precise analysis, the meaning of niche was difficult to clarify for the spatial case. For instance, Levins (1968) "...prefer to define niche as a fitness measure on an environment space" (p. 40). In our terminology, this would correspond to the tolerance vector $\mathbf{r}_0^{(i)}$. However, the same author in the same book calculates competition as an overlap between the spatial distributions of the populations (p. 51). It would correspond to our \mathbf{n} in the role of the resource utilization function. The issue has never become clearer since then, especially because terminological precision was not perceived as meaningful and reachable goal.

Here we provided the solid ground to decide. The impact and the sensitivity niche vectors are the precise descriptors. They are closely related to the spatial distribution of the population. In many cases, this distribution itself is an acceptable proxy for the niche. In contrast, the tolerance vector fails to take into account the consequences of migration.

The relevance of the issue was clearly demonstrated by Abrams and Wilson (2004). In their two-patch model, both species have the higher fitness (i.e., lower R^* value) at the same patch. Still, they may be able to coexist if their mobility is different. If the locally inferior species has a lower migration rate, then its better localization on the better patch may compensate for its local inferiority. Then, the different spatial distribution of the two species establishes a kind of niche segregation. It would be overlooked, if \mathbf{r}_i^0 was considered in the role of niche specification.

The environmental gradient (therefore, the scenopoetic niche axis of Hutchinson) can be considered as a limiting case of the linear chain of habitats. Technically, our analysis does not apply because of the infinitely many locations. Still, we expect our conclusions to remain valid provided, that a *finite* spatial interval is considered. The dynamical matrix would be replaced by a reaction-diffusion operator with a discrete spectrum (Shigesada and Kawasaki, 1997). Instead of the right and left eigenvectors we would have eigenfunctions specifying population distribution and the location-dependent reproductive value. The isolatedness of the dominant eigenvalue guarantees the validity of the perturbation expansion. See Durrett and Levin (1998) for a study of interspecific competition in such context. Mizera et al. (in prep.) studies the possibilities of niche-segregation along the gradient. Mizera and Meszéna (2003) analyses the possibility of evolutionary branching in this ecology; see Doebeli and Dieckmann (2003) for the corresponding speciation simulation.

Note that Diekmann et al. (1998, 2001) provided the precise general formulation for the theory of structured population that allows infinitely many i -states. While not discussed here, we expect our theory to generalize for their more general formalism.

Modeling of coexistence maintained by spatial heterogeneity was initiated by the seminal paper of Levene (1953), using population genetics context. Kisdi and Geritz (1999); Geritz and Kisdi (2000) continued the evolutionary study of Levene’s model by discussing emergence of reproductive isolation in this context. Meszéna et al. (1997) investigated adaptive dynamics and evolutionary branching in a continuous-time two-patch model. In this chapter this model is complemented by the impact/sensitivity niche description, and argued that the symmetry between habitat and functional niche segregation translates to a conceptual symmetry between allopatric and parapatric niche segregation. The purely ecological study of heterogeneity-maintained coexistence was initiated by Levin (1974); see Amarasekare (2003) for a recent review.

Chesson’s theory (Chesson, 2000b) suggest a deeper, unifying understanding of coexistence. Necessarily, any kinds of species coexistence are based on stabilizing effects. Resource partitioning is the simplest example for such mechanism. Fluctuations may result in two additional mechanisms, the “storage effect” and the “effect of relative nonlinearity” (Chesson, 1994). Both of them are related to the nontriviality of averaging. Therefore they are vanishing in a fully additive linear model, that behaves like its averaged counterpart (Chesson and Huntly (1997)). Chesson (2000a) extended the theory for spatially varying environment. The effects of storage and relative nonlinearity work identically to the previous case. However, spatial averaging results in an additional diversity-stabilizing effect, which is related to the spatial covariance between the local density and local growth rate.

Instead of the spatial averaging, we used the theory of structured populations. Still, the approach presented here is entirely consistent with Chesson’s one. The first and the second terms of our Eq. (3.22) correspond to his standardized environmental (\mathcal{E}) and competitive (\mathcal{C}) parameters, respectively. The additive linear construction of our model ensures, that both the storage effect and the effect of relative nonlinearity is vanishing. (The first one would correspond to non-additivity of the environmental and the competition parameter; the second one would mean a difference between the invader and the resident in the spatially averaged competition parameter.) Con-

sequently, the type of coexistence, which was studied here, is completely explained by the density-growth rate covariance. This conclusion is in line with the intuitive picture: The essential point is that a species maintain a higher density in the patch, in which its growth rate is higher. This covariance is diminishing at high migration rates. Small modifications of the current model would lead to reappearance of the other two effects. Still, the covariance effect seems to be the main issue in the investigated type of coexistence.

While Levene (1953) used the term “niche” for the two patches of his model, later fragmentation of the theory disconnected the specific studies of (spatial, or not) species coexistence from the verbal “niche theory”, mostly referring to Hutchinson’s niche axes. Still, development of coexistence theory has remained consistent with the original concept of competitive exclusion and niche segregation. Both Levins’s understanding on the role of regulating variables (Levin, 1970, 1974) and Chesson’s one on the need to be averaged differently point to the necessity for ecological differentiation. The expectation that space-time heterogeneity can weaken competition and de-emphasize the importance of segregation for coexistence was falsified (Chesson, 1991; Chesson and Huntly, 1997). The explicit interest towards niche theory, as the “central organizing aspect of modern ecology”, was rejuvenated by Leibold (1995). The investigation presented here closed the circle by mathematically connecting the spatial/structured coexistence problem to a formalized concept of competitive niche.

Our investigation was also motivated by the possible evolutionary consequences of the symmetry between the habitat and the functional types of niche segregation. Does the corresponding symmetry exist in the speciation modes also? The main stumbling block to study this issue is the lack of conceptual clarity of the notion of niche (Leibold, 1995). Here we made a step to rectify the situation by modeling the spatial niche segregation in a precise theoretical context of Meszéná et al. (2006). We learnt that the conditions of a significant niche segregation and of the possibility of evolutionary branching are analogous: Both of them requires sufficiently high difference between the habitats and sufficiently slow migration between them.

The evolutionary aspect was already dominant in Levene’s (1953) seminal paper about the population genetical consequences of environmental heterogeneity. He demonstrated that spatial heterogeneity can maintain genetic polymorphism. The way of regulation was the essential issue: Polimorphysm can be maintained only

in case of separate regulation in the various habitats (Christiansen, 1975). The analogous problem with functional niche segregation was studied by Christiansen and Loeschcke (1980a,b). These investigations assumed random mating, which precluded emergence of species diversity.

Adaptive dynamics introduced a significant simplification by separating the study of frequency dependence from the complications of diploid genetics. In clonal models it is clear that the diversity-maintaining effect of niche segregation may lead to evolutionary branching, if the negative frequency-dependence is strong enough. Branching evolution in the Lotka–Volterra model was demonstrated already in Metz et al. (1996). Following Meszéna et al. (1997), here we showed that, in a two patch environment, evolutionary branching can be initiated either by decreasing the migration rate between patches or by increasing the difference between them. The first one is reminiscent to allopatric speciation, initiated by a newly emerging migration barrier. The second one is a clonal equivalent of parapatric speciation, when no migration barrier emerges. In genetic modeling, Dieckmann and Doebeli (1999) demonstrated the possibility of adaptive speciation, Doebeli and Dieckmann (2003) dealt with the case of environmental gradient. While a similar analysis is still to be done for the two-patch case, based on the already existing results, we expect the adaptive dynamical results to be indicative for the possibility of the adaptive parapatric and allopatric speciation.

If arrested gene flow were a prerequisite of speciation, parapatric speciation would be just as impossible as the sympatric one. In the context of adaptive speciation, however, the sympatric (based on functional niche segregation), the parapatric and the allopatric modes of speciation are on equal footing: all of them are adaptations to different ways of niche segregations. This way we hope to find a biologically plausible unifying concept for all speciation modes.

Chapter 5

Limiting similarity in fluctuating environment

This chapter is based on the article:

A. Szilágyi, G. Meszéna: *Coexistence in a fluctuating environment by the effect of relative nonlinearity: a minimal model*. Journal of Theoretical Biology (under review)

Introduction

The role of environmental fluctuations in maintenance of species diversity is one of the most frequently investigated topics in theoretical ecology. In this chapter we investigate the applicability and usefulness of the model independent definition of niche proposed by Meszéna et al. (2006), summarized briefly in Chapter 2, in a fluctuating environment.

Hutchinson (1961) had already questioned the universal validity of the equilibrium coexistence theory and raised the question whether the high diversity of plankton communities could be explained by either the fluctuating nature of the environment or the internal dynamics of the system. Indeed, Armstrong (1976) demonstrated that the number of coexisting species can exceed the number of resources even in a constant environment if the population dynamical attractor is not a fixed point. During the '80s it has become a widely held opinion that the Hutchinson–MacArthur-era overestimated the relevance of competitive exclusion compared with nonequilibrium processes (Huston, 1979, 1994; Begon et al., 1996). On the other hand, Abrams (1983); Chesson (1991); Chesson and Huntly (1997); Chesson et al. (2004) stressed that fluctuations do not alleviate the need for ecological segregation. Even in a fluctuating environment the species having the largest long-term rate of increase (calculated via proper averaging) will outcompete the others. Therefore, competitive exclusion remains the default behavior.

According to Chesson (2000b), coexistence must be stabilized by a negative feedback that gives a boost to any of the populations that become rare via perturbation. In a constant environment, niche segregation of the classical kind provides this feedback: the rare species will have an abundant supply of resources. For fluctuating environments Chesson (1994) enlists two additional mechanisms that are specifically related to fluctuations: the “storage effect” and the “effect of relative nonlinearity”. The first one is essentially a temporal niche-segregation, made possible by the fluctuations (Christiansen and Fenchel, 1977, p. 69, Amarasekare, 2003), while the second one means that some parameters of the fluctuations (like the variance) emerge as additional regulating variables via the non-triviality of non-linear averaging (cf. Levins, 1979; Kisdi and Meszéna, 1993). The spatiality-related coexistence mechanisms, described in Chesson, 2000a; Amarasekare, 2003; Amarasekare et al., 2004 and in the

previous chapter, are outside of our interest here.

Turelli (1978) emphasized the importance of stabilizing feedbacks as sufficient conditions for coexistence. If either of the two populations are able to grow (i.e. if it has a positive average growth rate) when rare enough, they are certainly able to coexist. This criterion of mutual invasibility is widely used to simplify theoretical studies of coexistence.

In this chapter we reconnect the theory of fluctuation-mediated coexistence with the classical notion of niche and limiting similarity on a clear mathematical basis. While we aim for the general picture, here we use the simplest model that we could conceive to demonstrate the principal connection between equilibrium and nonequilibrium ecology (see Parvinen and Meszéna, 2009 for a more realistic model of disturbance-generated coexistence in the same vein). For this purpose we use a slightly generalized version of the relative nonlinearity-type coexistence model by Kisdi and Meszéna (1993). There are only two regulating variables in this model, the long-term average and the variance of the total density. Therefore, it is ensured that at most two species can coexist. Because of its simplicity, analytical treatment of the model is possible via the method of moment closure. We will compare these results with numerical simulations.

5.1 Building the model

Since we wish to study principal issues, we look for a model of fluctuation-mediated coexistence as close to analytical tractability as possible. Continuous time is preferred, as discrete-time population dynamics tends to exhibit more complicated behavior. The simplest source of fluctuations is the uncorrelated external noise. We expect competitive exclusion to operate in the absence of fluctuations. This is ensured if the dependence on the total density is the only regulating feedback in the model (density-dependent selection, MacArthur, 1962). If density-dependence were linear, fluctuations would not affect the behavior (Chesson and Huntly, 1997). Quadratic dependence is the minimalist route to the effect of relative nonlinearity.

Therefore, the fluctuations will be driven by a Gaussian uncorrelated (white) noise $\xi(t)$ with zero mean ($\overline{\xi} = 0$, the overline denotes time averaging). Its autocorrelation

function can be written as

$$\overline{\xi(t_1)\xi(t_2)} = \delta(t_1 - t_2), \quad (5.1)$$

where $\delta(t_1 - t_2)$ is the “Dirac-delta function”, that is zero for $t_1 \neq t_2$, but has an integral of 1, specifying the normalization.

Then, our model is defined by the stochastic differential equation¹

$$\frac{d}{dt}n_i(t) = \overbrace{\left[\sigma_i \xi(t) - a_i(n(t) - K_i) - b_i(n(t) - K_i)^2 \right]}^{r_i(t)} n_i(t), \quad (5.2)$$

where $n_i(t)$ is the density of Species i at time t , $n(t) = \sum_i n_i(t)$ is the total density. The expression in the square bracket, denoted by $r_i(t)$, is the instantaneous growth rate of Species i . K_i is the carrying capacity of the i th Species, i.e. the equilibrium density without noise; a_i , b_i and σ_i are positive constants. The ratio b_i/a_i characterizes the nonlinearity of population regulation, while the noise-intensity coefficient σ_i specifies the dependence of the population on the external fluctuations. To avoid complications arising from an Allee-effect, we want the deterministic part of the growth rate to decrease monotonously with increasing density. To this end, the parameter values are chosen to satisfy the inequality

$$\frac{a_i}{2b_i} > K_i. \quad (5.3)$$

Since white noise can change arbitrarily fast, the interpretation and simulation of a stochastic differential equation needs extra care (May, 1973, p. 204; Braumann, 2007). We assume that in the real word the fluctuations are correlated, i.e. it cannot change arbitrarily fast. Then, we assume that the correlation time is short compared to the timescale of population dynamical effects. Therefore, we study the limit of zero correlation time, as specified by Eq. (5.1), leading to the so-called Stratonovich-interpretation of Eq. (5.2) (Braumann, 1999). It is something different than considering the continuous-time process as a limiting case of a discrete dynamics with independent and identically distributed (i.i.d.) random variables as noise (Itô-interpretation, Feldman and Roughgarden, 1975).

More precisely, as the two interpretations differ only by a correction term, any situation can be described via either of them if the ingredients are defined appropriately. However, only the Stratonovich interpretation has the property that the

¹For notational convenience in this chapter we denote species indices by subscript.

long-term stationary state can be characterized by the natural “equilibrium” condition $\bar{r}_i = 0$. Therefore, the Stratonovich formulation is the more intuitive way to describe continuous stochastic population dynamics. We have to take care of the discrepancy between the Itô and Stratonovich limits for the numerical simulations.

One can calculate the time-average of the instantaneous growth rate as

$$\bar{r}_i = -a_i(\bar{n} - K_i) - b_i \overline{(n - K_i)^2} + \sigma_i \bar{\xi} = -a_i(\bar{n} - K_i) - b_i(\bar{n} - K_i)^2 - b_i V, \quad (5.4)$$

where we denote the variance of the total density n by $V = \overline{n^2} - \bar{n}^2$. (Overline means averaging in the sense consistent with the Stratonovich calculus.) Observe the detrimental effect of the fluctuations on the long-term growth rate through the quadratic term. The “equilibrium” condition $\bar{r}_i = 0$ should hold for any species that survives for a long period of time.

Without fluctuations, $V = 0$. Then \bar{r}_i becomes zero when the time-averaged total density \bar{n} reaches the carrying capacity K_i . By the well-known argument of MacArthur (1962), competition is won by the species with the highest carrying capacity in this case.

In the presence of external fluctuations the densities will also fluctuate, implying $V > 0$. The average growth rates are receiving feedback through two “regulating” variables: \bar{n} and V . Each surviving population provides one equilibrium equation ($\bar{r}_i = 0$ for Species i) for these variables. The generic solution exists only if the number of equations does not exceed the number of unknowns. That is, coexistence of two, but not more, species is allowed in this model.

Since this bound on diversity is clear from the onset of our investigations, it is instructive to write down the dynamics (5.2) again just for two species:

$$\frac{d}{dt} n_1(t) = \left[\sigma_1 \xi(t) - a_1(n(t) - K_1) - b_1(n(t) - K_1)^2 \right] n_1(t), \quad (5.5)$$

$$\frac{d}{dt} n_2(t) = \left[\underline{\sigma_2 \xi(t)} - a_2(n(t) - K_2) - \underline{b_2(n(t) - K_2)^2} \right] n_2(t). \quad (5.6)$$

The special case $b_2 = \sigma_2 = 0$, i.e. when the underlined terms are deleted, will be referred to as the simplified model, first published by Kisdi and Meszéna (1993). Since we are interested in limiting similarity here, we need the full model that will allow the two species to become equivalent when their parameters are equal. However, as the simplified model has a fewer number of parameters, it is more convenient for the study of the coexistence of two species that are distinct.

5.2 Elementary analytic results

In this Section we summarize the analytical results that do not rely on the moment closure approximation; the latter will be considered in Section 5.4. The calculations presented here are direct consequences of the equilibrium conditions. While they are valid for arbitrarily large fluctuations, we will often use the approximation of small fluctuations to keep the formulae transparent.

5.2.1 Single species

First we consider the long-term equilibrium of a single species. The equilibrium condition can be written as

$$\bar{r} = -a(\hat{n} - K) - b(\hat{n} - K)^2 - b\hat{V} = 0 \quad (5.7)$$

(cf. Eq. (5.4)), where \hat{n} and \hat{V} denote the average and the variance of the population density, respectively, for the case of a lone population. In a constant environment $\hat{V} = 0$, implying $\hat{n} = K$. As density variance has a negative effect on the growth rate and there is no Allee effect (monotonicity condition (5.3)), the average density must decrease with increasing density fluctuation.

For small fluctuations we expect a small \hat{V} and therefore a small value of $\hat{n} - K$ characterizing the departure of the average density from the constant-environment value. Then the second term of Eq. (5.7) will be of second order and thus small; neglecting it leads to the relation

$$\hat{n} = K - \frac{b}{a}\hat{V}, \quad (5.8)$$

that is valid for small fluctuations only.

Note that the terms, like the second one in Eq. (5.7), will always be negligible for small fluctuations. Therefore, the essential role of the nonlinear terms $-b_i(n_i - K_i)^2$ in dynamics (5.7) is to implement a sensitivity towards the fluctuations on the density. The ratio b/a that measures the nonlinearity of the density dependence also characterizes the sensitivity of the average density towards density fluctuations. In the case of linear density dependence ($b = 0$), fluctuations of the density average out; the average density will not be affected by the fluctuations.

5.2.2 Mutual invasion

The condition of mutual invasibility of two species reads

$$\begin{aligned}\rho_1 &= -a_1(\hat{n}_2 - K_1) - b_1(\hat{n}_2 - K_1)^2 - b_1\hat{V}_2 > 0, \\ \rho_2 &= -a_2(\hat{n}_1 - K_2) - b_2(\hat{n}_1 - K_2)^2 - b_2\hat{V}_1 > 0.\end{aligned}\tag{5.9}$$

Here ρ_i denotes the “boundary” growth rate of Species i , i.e. its growth rate, when it is rare and the other species fluctuates in a stationary manner. While these conditions are exact, the quantities \hat{n}_i and \hat{V}_i cannot be calculated analytically without the moment closure approximation of Section 5.4.

A more concise condition can be derived for the simplified model with $b_2 = \sigma_2 = 0$. In this case Species 2 is affected by the fluctuations only through its interaction with Species 1. When alone, Species 2 assumes an equilibrium density determined by the condition $\bar{r}_2 = -a_2(\hat{n}_2 - K_2) = 0$, implying $\hat{n}_2 = K_2$. Then the boundary growth rate of Species 1 is

$$\rho_1 = -a_1(K_2 - K_1) - b_1(K_2 - K_1)^2.\tag{5.10}$$

It is positive iff

$$K_2 < K_1,\tag{5.11}$$

where inequality (5.3) was used. On the other hand, Species 2 has a positive boundary growth rate against the established population of Species 1 iff

$$\rho_2 = -a_2(\hat{n}_1 - K_2) > 0.\tag{5.12}$$

The combination of Eqs. (5.10) and (5.12) provides the necessary and sufficient condition for mutually invasibility as

$$\hat{n}_1 < K_2 < K_1\tag{5.13}$$

(cf. Kisdi and Meszéna, 1993). There is no exact analytic way to determine \hat{n}_1 ; it has to come either from simulations or from moment closure approximation applied to a single species.

5.2.3 Advantage of rarity

Advantage when rare is an essential component of coexistence, i.e. negative frequency dependence. Without frequency dependence, $\rho_1 > 0$ would imply $\rho_2 < 0$, and vice

versa. Therefore, negative frequency dependence can be measured by a quantity like $\rho_1 + \rho_2$. It turns out that

$$\rho = \frac{\rho_1}{a_1} + \frac{\rho_2}{a_2} \quad (5.14)$$

is the good measure for which a transparent formula can be derived. Mutual invasibility implies $\rho > 0$. We will use the approximation of small fluctuations. Straightforward calculation leads to the form

$$\rho = \left[\frac{b_1}{a_1} - \frac{b_2}{a_2} + 2 \frac{b_1 b_2}{a_1 a_2} \Delta K \right] (\hat{V}_1 - \hat{V}_2) - \left[\frac{b_1}{a_1} + \frac{b_2}{a_2} \right] (\Delta K)^2 > 0, \quad (5.15)$$

where the notation

$$\Delta K = K_1 - K_2 \quad (5.16)$$

was introduced. For $\Delta K = 0$ it simplifies to

$$\left(\frac{b_1}{a_1} - \frac{b_2}{a_2} \right) (\hat{V}_1 - \hat{V}_2) > 0. \quad (5.17)$$

Condition (5.17) represents the coexistence-stabilizing mechanism in an intuitively appealing way. As mentioned above, the ratio b_i/a_i measures the nonlinearity of density-dependence of Species i ; their difference in the first factor is the “relative” nonlinearity (Chesson, 1994, 2000b). Phrasing it differently, the first factor represents the difference between the species in their dependence on the two regulating variables, the average \bar{n} and the variance V of the total density. On the other hand, the second term is the difference between the species in their strength of making the total population size fluctuate. For coexistence, the species must differ in both respects. Moreover, they must differ in these aspects in the same way. The species that makes n more fluctuating must be the one that is more sensitive to the fluctuations of n . The species that affects the regulating variable V must be the one that is also more sensitive toward V . Like in constant-environment resource partitioning, this arrangement ensures rare advantage and stabilizes coexistence. We will revisit this intuitive expectation in Section 5.5.1 in a more precise way.

Obviously, conditions (5.15–5.17) provide only the necessary, and not the sufficient conditions for mutual invasibility. They represent the conditions for having a tendency for rare advantage. If the parameter choices (esp. of ΔK) are such that one species has a large advantage, then it is possible that the inferior species will be unable to invade despite its advantage gained from rarity.

5.2.4 Coexistence

Assume now that the two species coexist. Then their long-term growth rates satisfy the equilibrium equations

$$\begin{aligned}\bar{r}_1 &= -a_1(\bar{n} - K_1) - b_1(\bar{n} - K_1)^2 - b_1V = 0, \\ \bar{r}_2 &= -a_2(\bar{n} - K_2) - b_2(\bar{n} - K_2)^2 - b_2V = 0.\end{aligned}\tag{5.18}$$

These (quadratic) conditions determine the equilibrium values of the regulating variables \bar{n} and V via a 4th order algebraic equation. We write down the solution for small fluctuations only. For $V = 0$ coexistence is possible only if $K_1 = K_2$; the solution is characterized by $\bar{n} = K_1 = K_2$. Therefore, we expect that $K_1 \sim K_2$ is required for small V and then $K_1 \sim \bar{n} \sim K_2$. Therefore the second term in both equations are of second order and therefore small; neglecting them leads to

$$\bar{n} = \frac{a_1b_2K_1 - a_2b_1K_2}{a_1b_2 - a_2b_1}\tag{5.19}$$

and

$$V = \frac{K_1 - K_2}{\frac{b_1}{a_1} - \frac{b_2}{a_2}}.\tag{5.20}$$

Note the consistence of these formulae with the assumptions we made: smallness of V implies smallness of $K_1 - K_2$ as a condition for coexistence. The analogue of Eq. (5.8),

$$\bar{n} = K_i - \frac{b_i}{a_i}V,\tag{5.21}$$

remains valid for the two-species case by the same argument from which it was derived in Section 5.2.1.

For the simplified model,

$$\bar{n} = K_2\tag{5.22}$$

and

$$V = \frac{a_1}{b_1}\Delta K\tag{5.23}$$

applies.

5.3 Coexistence: simulation results

For simulation purposes, the continuous dynamics (5.2) is discretized as

$$n_{i,t+\Delta t} - n_{i,t} = \left[-a_i(n_t - K_i) - b_i(n_t - K_i)^2 + \frac{1}{2}\sigma_i^2 \right] n_{i,t}\Delta t + \sigma_i n_{i,t}\sqrt{\Delta t}\xi_t,\tag{5.24}$$

where $n_{i,t}$ and n_t denote the density of Species i and the total density, respectively, at time t . The noise ξ_t is an i.i.d. process of variance 1 for time steps of length Δt . The scaling factor $\sqrt{\Delta t}$ in the random term ensures that the normalization (5.1) is obeyed in the $\Delta t \rightarrow 0$ limit. The last term in the square bracket is the correction characteristic of Stratonovich integration (see Appendix D; Sethi and Lehoczky, 1981; Stratonovich, 1989; Braumann, 2007). Without it, the limit of the discrete dynamics would correspond to the Itô-interpretation of the stochastic differential equation (5.2) (cf. Smythe et al., 1983).

A simulated time series of two coexisting species is plotted in Fig. 5.1 for a set of parameters satisfying the mutual invasibility condition. In line with the invasibility prediction, they coexist for an arbitrary long period of time. Nevertheless, one should note that the densities fluctuate by many orders of magnitude. The populations experience extremely low densities.

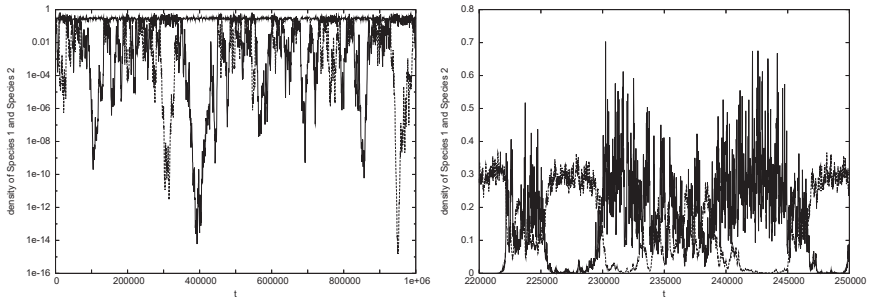


Figure 5.1: Time course of the densities of the two coexisting species. The left pane with logarithmic vertical scale demonstrates the repeated occurrence of extremely low densities, incompatible with realistic population sizes. A part of the same curve is presented with linear scale on the right pane. Parameters: $a_1 = a_2 = b_1 = 0.1$; $b_2 = 0.02$; $\sigma_1 = 0.1$; $\sigma_2 = 0.05$; $K_1 = 0.3$; $K_2 = 0.298$. The same parameters are used for the rest of the Figures unless indicated otherwise.

Excursions to low densities warrants introduction of an extinction threshold. This way extinction of one of the species becomes a probability 1 event; the possibility of coexistence for infinite time is lost. Then the appropriate question is the expected length of coexistence.

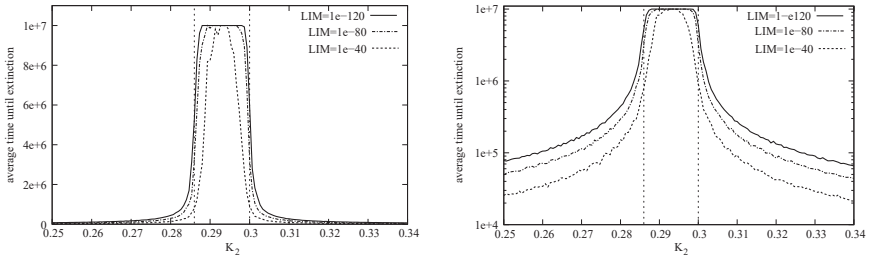


Figure 5.2: Expected time until extinction of one of the co-occurring species in the presence of an extinction threshold (LIM) as a function of the carrying capacity K_2 (simplified model, average of 50 runs). Vertical (time) scale is linear on the left plot and logarithmic on the right one. The simulations were terminated at time $T = 10^7$ if no extinction occurred. The region of mutual invasibility (\hat{n}_1, K_1) is shown by the vertical dashed lines. For extremely low extinction thresholds the parameter region of long-term coexistence coincides with that range. For more realistic thresholds, the possibility for coexistence is more restricted. Parameters are the same as in Fig. 5.1 except that now $b_2 = \sigma_2 = 0$. This parameter choice is maintained in later figures of the simplified model when not indicated otherwise. The equilibrium density of Species 1, when alone, is measured to be $\hat{n}_1 = 0.286$.

Fig. 5.2 presents the average time until one of the densities goes below the threshold as a function of K_2 for different threshold values. Since the simplified model is used, condition (5.13) provides the parameter range for mutual invasibility, depicted by vertical dashed lines. Note that the plateau on the top of the curves is an artifact of terminating the simulations at $T_{\max} = 10^7$ time steps. Fig. 5.4 shows the average length of coexistence as a function of the extinction threshold. The two curves represent two parameter sets that do and do not allow for mutual invasibility. In the first case the length of coexistence – after a transient period – increases linearly as a function of the inverse of the extinction threshold. In contrast, the expected time until extinction increases very slowly and remains essentially bounded when the condition of mutual invasibility is not met.

The presented results confirm the prediction of the mutual invasibility criterion unequivocally for sufficiently low extinction thresholds. The expected length of coexistence is bounded only by the simulation time T_{\max} where the condition is met, but falls off by orders of magnitude outside the range of mutual invasibility. On the other hand, one should note that the “sufficiently low” extinction threshold is unrealistically low from biological point of view. The extinction threshold 10^{-20} , i.e. population size 10^{20} is required for coexistence length 10^6 even in case of mutual invasibility. For realistic population sizes the period of coexistence is very short.

The extreme level of density fluctuations are presumably related to the low-frequency components of the white noise. Therefore, introduction of a low-frequency cutoff of the power spectrum would make our model a good candidate for describing real species coexistence. As a proof of concept, Fig. 5.3 presents the behavior of the model with a sinusoid, instead of white-noise, perturbation with $\xi_i(t) = \sin(\omega t)$. Without analyzing the results in detail the conclusion is evident: the fluctuations of the density of the species remains in a biologically acceptable range (Fig. 5.3). The parameters do not need fine-tuning, coexistence is robust.

However, for the rest of the current model, we remain interested in the analytic study of the white-noise model in the hope for insights that remain valid for more parameter-rich models.

5.4 Moment closure approximation

The equilibrium equations (5.18) are insufficient to fully determine the statistics of the population fluctuations. When a population is considered alone (Section 5.2.1), this condition establishes a relation between the average and the variance of the density, but does not allow us to calculate these quantities separately. For two populations, the average and variance of the sum of the densities are obtainable (Section 5.2.4), but not the statistics of the two populations separately.

For more detailed analytic results the moment closure approximation will be used: we assume small fluctuations and neglect the third and higher statistical moments of the fluctuating variables.

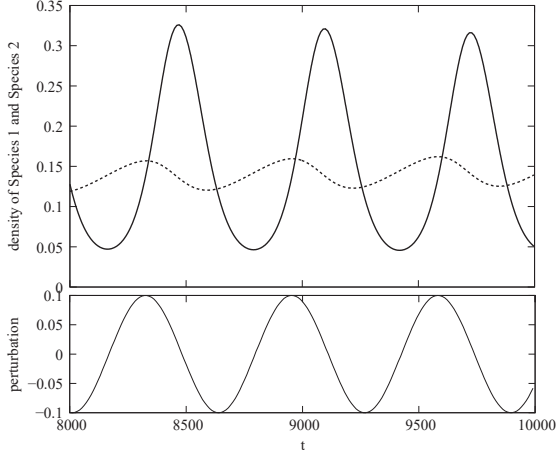


Figure 5.3: *Time course of the simplified model perturbed by a correlated (sinusoidal) noise: $\xi(t) = \sin(\omega t)$ with $\omega = 0.01$. Top: periodic time course of densities. Bottom: the perturbing function $\sigma_1 \xi(t)$.*

5.4.1 Single species

The long-term average of the time-derivative of any quantity, which remains bounded, should be zero. Applying this principle to the logarithmic density $\ln n$ (time derivative of which is the growth rate r) leads to the equilibrium condition $\bar{r} = 0$. We have exploited this condition already in Section 5.2.1. We need an additional relation to proceed further. For this purpose here we consider the average of the time derivative of n , instead of $\ln n$:

$$\overline{\frac{d}{dt}n(t)} = \bar{rn} = \overline{[\sigma\xi(t) - a(n(t) - K) - b(n(t) - K)^2]n} = 0. \quad (5.25)$$

We will rewrite this condition in terms of the departure from the average

$$m(t) = n(t) - \hat{n}. \quad (5.26)$$

By definition,

$$\overline{m(t)} = 0 \quad (5.27)$$

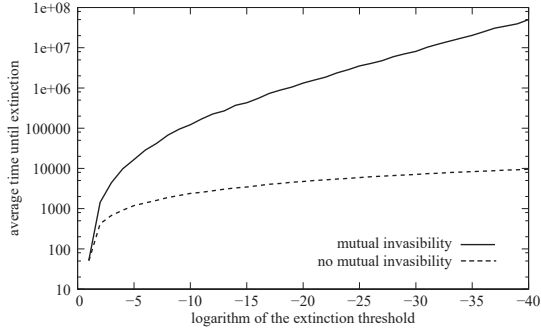


Figure 5.4: *Expected time until extinction as a function of the extinction threshold (simplified model, average of 500 runs). Continuous line: $K_2 = 0.29$ satisfying the condition for mutual invasibility. The coexistence time diverges for low thresholds and becomes inversely proportional to the threshold. Dotted line: $K_2 = 0.19$, no mutual invasibility. Coexistence time remains essentially bounded.*

and

$$\overline{m(t)^2} = \hat{V}. \quad (5.28)$$

The moment closure approximation, valid for small fluctuations only, is defined by neglecting higher moments of m . In particular, we will assume

$$\overline{m(t)^3} = 0. \quad (5.29)$$

Moreover, we state that

$$\overline{m\xi} = \frac{\sigma}{2}\hat{n}. \quad (5.30)$$

This relation is a consequence of the Itô vs. Stratonovich dichotomy. The average of $m\xi$ is zero in the Itô-interpretation because the momentary value of m depends only on the values of ξ s in the previous time steps. The Stratonovich average, which is the relevant one for us, differs from that value by a correction term leading to Eq. (5.30) (see the Appendix D for details).

When the relationships (5.26–5.30) are taken into account, the rewritten version of condition (5.25) reads

$$\frac{\sigma^2}{2}\hat{n} - a\hat{n}(\hat{n} - K) - a\hat{V} - b\hat{n}(\hat{n} - K)^2 - b\hat{n}\hat{V} - 2b\hat{V}(\hat{n} - K) = 0. \quad (5.31)$$

As the moment closure approximation is valid for small fluctuations anyway, we use the small-fluctuation result (5.8). Substituting $\hat{n} - K$ in Eq. (5.31) with $-(b/a)\hat{V}$ and neglecting the second-order terms in \hat{V} leads to

$$\frac{\sigma^2}{2}\hat{n} = a\hat{V}. \quad (5.32)$$

Then we combine this result with Eq. (5.8) and arrive to

$$\hat{V} = \frac{\sigma^2 a K}{2a^2 + \sigma^2 b} \quad (5.33)$$

and

$$\hat{n} = \left(1 - \frac{\sigma^2 b}{2a^2 + \sigma^2 b}\right) K = \frac{2a^2 K}{2a^2 + \sigma^2 b}. \quad (5.34)$$

Comparison of this result with numerical simulations is presented in Fig. 5.5. The coincidence of the predicted and simulated average densities is remarkable; the fluctuations need not to be extremely small for this. The moment closure method turns out to be reliable as long as the noise intensity parameter σ is not larger than the parameters a and b in the regulation terms.

Observe that the equilibrium density is a monotonically decreasing function of the strength of the external fluctuations. With very high fluctuations the average density can be made arbitrary small, provided that the extinction threshold is small enough.

5.4.2 Equilibrium of two coexisting species

Here we repeat the approach of Section 5.4.1 for two species. Analogously to Eq. (5.25), from Eq. (5.2) we write

$$\overline{\frac{d}{dt}n_i(t)} = \overline{r_i n_i} = \overline{[\sigma_i \xi(t) - a_i(n(t) - K) - b_i(n(t) - K)^2] n_i} = 0. \quad (5.35)$$

We introduce the deviation $m_i = n_i - \bar{n}$ and use the notation $m = m_1 + m_2 = n - \bar{n}$. Note that

$$\overline{m^2} = \overline{m_1 m} + \overline{m_2 m} = V. \quad (5.36)$$

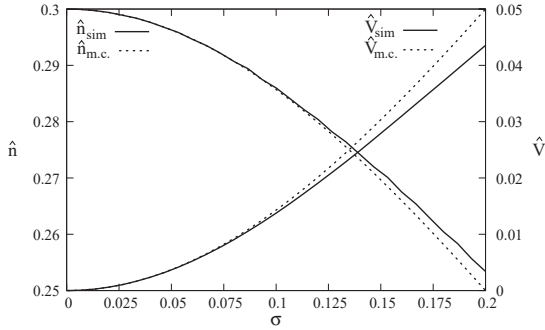


Figure 5.5: Average density (\hat{n}) and variance (\hat{V}) of a single population as a function of the fluctuation strength σ . The moment closure method (dashed line) approximates the simulation results (solid line) very well for $\sigma < 0.1$ and reasonably well for $0.1 < \sigma < 0.2$. Parameters: $a = 0.1, b = 0.1, K = 0.3$.

Analogously to Eq. (5.30), the Stratonovich nature of averaging implies

$$\overline{m_i \xi} = \frac{\sigma_i}{2} \overline{n_i} \quad (5.37)$$

(see the Appendix D). Repeating the calculation which leads to Eq. (5.31), we arrive at

$$\frac{\sigma_i^2}{2} \overline{n_i} - a_i \overline{n_i} (\overline{n} - K_i) - a_i \overline{m_i m} - b_i \overline{n_i} (\overline{n} - K_i)^2 - b_i \overline{n_i} V - 2b_i \overline{m_i m} (\overline{n} - K_i) = 0, \quad (5.38)$$

where the term $\overline{m_i m^2}$ was neglected per the moment closure approximation.

Now we substitute Eq. (5.21) into the expressions $(\overline{n} - K_i)$ and neglect all second order terms in V . We arrive at the equality

$$\frac{\sigma_i^2}{2} \overline{n_i} = a_i \left(1 - \frac{2b_i}{a_i} V \right) \overline{m_i m}. \quad (5.39)$$

Here the second term in the bracket, being proportional to V , is small compared to the first one. Neglecting it leads to

$$\frac{\sigma_i^2}{2a_i} \overline{n_i} = \overline{m_i m}. \quad (5.40)$$

Summation of this formula for $i = 1, 2$ leads to the equation

$$V = \frac{\sigma_1^2}{2a_1} \bar{n}_1 + \frac{\sigma_2^2}{2a_2} \bar{n}_2 = v_1 \bar{n}_1 + v_2 \bar{n}_2, \quad (5.41)$$

where the notation

$$v_i = \frac{\sigma_i^2}{2a_i} \quad (5.42)$$

was introduced. Note the intuitive meaning of v_i : it is the *per capita* contribution of Species i to the variance of the total population size. Observe the consistency with the single species result (5.32). Equation (5.41), together with the trivial relation

$$\bar{n} = \bar{n}_1 + \bar{n}_2 \quad (5.43)$$

establishes the connection between the average densities of the two species and the two regulating variables. One can solve the system of equations (5.41)(5.43) for the average densities:

$$\begin{aligned} \bar{n}_1 &= \frac{V - v_2 \bar{n}}{v_1 - v_2}, \\ \bar{n}_2 &= \frac{-V + v_1 \bar{n}}{v_1 - v_2}. \end{aligned} \quad (5.44)$$

These results, together with equations (5.19–5.20), provide all the interesting quantities as a function of the model parameters.

For the simplified model, substitution of $b_2 = \sigma_2 = 0$ and Eqs. (5.22–5.23) lead to

$$\begin{aligned} \bar{n}_1 &= \frac{2a_1^2}{b_1 \sigma_1^2} \Delta K = \frac{\hat{n}_1}{K_1 - \hat{n}_1} \Delta K, \\ \bar{n}_2 &= K_2 - \frac{2a_1^2}{b_1 \sigma_1^2} \Delta K = K_2 - \frac{\hat{n}_1}{K_1 - \hat{n}_1} \Delta K. \end{aligned} \quad (5.45)$$

These results are compared with the numerical simulations in Fig. 5.6. The departure of the moment closure prediction from the simulated values is larger than it was for a single species. Still, the agreement is reasonable. The moment closure approximation seems to capture the essential behavior of the system. Observe that the deviation is the same in magnitude, but opposite in direction, for the two species. That is, the total density is still provided accurately; the moment closure method is less precise in predicting the ratio of the two densities. This situation is understandable in the light of high sensitivity of the relative densities for the fluctuations.

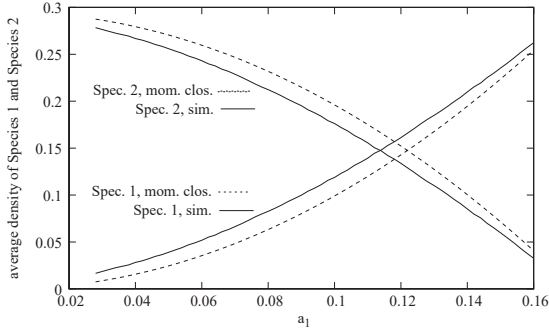


Figure 5.6: Average densities of two coexisting species as a function of a_1 in the simplified model. The difference between the moment closure (dashed lines) and the simulated (solid lines) densities are significantly larger than in the single species case of Fig. 5.5. Still, moment closure remains a reasonable approximation. $K_2 = 0.295$, within the range of mutual invasion.

5.5 Niche segregation and the robustness of coexistence

5.5.1 Impact and sensitivity niches in our system

Based on the analytic results above, in this section we reinvestigate the model in the context of the theory of limiting similarity by Mesz  na et al. (2006), described briefly in Chapter 2. The sensitivity analysis is based on the assumption of equilibrium in an essential way. Its applicability for our model is not trivial.

A part of the framework is easy to translate. The growth rate r_i of the constant environment model should be replaced by the averaged growth rate \bar{r}_i because the “equilibrium” equation $\bar{r}_i = 0$ holds even in our variable environment. As we discussed already, the averaged total density \bar{n} and the variance of the total density V play the role of regulating variables: these quantities determine the \bar{r}_i s unequivocally.

Therefore, the vector of regulating factors can be written as

$$\mathbf{I} = \begin{pmatrix} \bar{n} \\ V \end{pmatrix}, \quad (5.46)$$

while the sensitivity vectors are

$$\mathbf{S}_i = - \begin{pmatrix} \frac{\partial r_i}{\partial \bar{n}} \\ \frac{\partial r_i}{\partial V} \end{pmatrix} = \begin{pmatrix} a_i + 2b_i(\bar{n} - K_i) \\ b_i \end{pmatrix}. \quad (5.47)$$

For small fluctuations, when $\bar{n} - K_i$ is small by (5.21), the formula simplifies to

$$\mathbf{S}_i \approx \begin{pmatrix} a_i \\ b_i \end{pmatrix}. \quad (5.48)$$

One can say that the coefficients of the linear and the quadratic density dependence measure the sensitivity towards the average and the variance of the total population size, respectively.

As we introduced in Section 2.2 the sensitivity of the equilibrium population sizes towards the additional mortalities can be determined by implicit differentiation of the equilibrium equation $r_i = r_i(\mathbf{I}(n_1, n_2, \dots, n_L), \mathbf{E}) = 0$ (cf. Eq. (2.16))

$$\frac{\partial n_i^e}{\partial \mathbf{E}} = - \sum_{j=1}^L (a^{-1})_{ij} \frac{\partial r_j}{\partial \mathbf{E}} = - \frac{1}{J} \sum_{j=1}^L \text{adj}(a)_{ij} \frac{\partial r_j}{\partial \mathbf{E}}. \quad (5.49)$$

The nontrivial part is the interpretation of the equilibrium density n_i^e . The average density \bar{n}_i is the obvious candidate. However, the average density of the species alone does not determine the regulating vectors. Therefore, the impact vectors cannot be defined, and the formalism cannot be applied without further considerations.

To apply the framework we have to restrict the possibilities of the stochastic dynamics to a two-parameter sub-family that can be parameterized by \bar{n}_1 and \bar{n}_2 . We do this by picking up the carrying capacities K_1 and K_2 as competitive parameters (Abrams, 1983), playing the role of the vector \mathbf{E} above. All other model parameters are regarded as fixed; robustness of coexistence is considered with respect to changes of the carrying capacities. This way both the average densities \bar{n}_1 , \bar{n}_2 and the regulating variables \bar{n} , V become functions of the carrying capacities K_1 , K_2 . Inversion of these relationships leads to an unequivocal definition of the dependence of the regulating variables on the average densities. Note that a similar reduction of

dimensionality was applied when population structure caused an analogous problem see previous chapter.

Then the impact niche vector of Species i is calculable from the relations (5.41) and (5.43) as

$$\mathbf{C}_i = \begin{pmatrix} \frac{\partial \bar{n}}{\partial \bar{n}_i} \\ \frac{\partial V}{\partial \bar{n}_i} \end{pmatrix} = \begin{pmatrix} 1 \\ v_i \end{pmatrix}. \quad (5.50)$$

From the vectors \mathbf{S}_i and \mathbf{C}_j we can obtain the competition matrix:

$$a_{ij} = -\frac{\partial r_i}{\partial \bar{n}_j} = \mathbf{S}_i \cdot \mathbf{C}_j. \quad (5.51)$$

As explained in Section 2.2, the determinant of this matrix is the measure of the robustness we are looking for:

$$\frac{\det(\mathbf{a})}{a_1 a_2} = \left(\frac{b_1}{a_1} - \frac{b_2}{a_2} + 2 \frac{b_1 b_2}{a_1 a_2} \Delta K \right) (v_1 - v_2). \quad (5.52)$$

Note that the scaling $a_1 a_2$ is the determinant of the competition matrix when fluctuations and the quadratic density dependence are absent, which is a kind of reference case. Observe resemblance of this measure of regulatedness to the quantity ρ in the l.h.s. of the necessary condition (5.15) in Section 5.2.3 for coexistence.

While invasion from rarity was considered in Section 5.2.3, here we studied the effect of a small perturbation. This difference in the approaches explains the discrepancies between the results. First, while the per capita fluctuation-producing effect of the species (v_1 and v_2) appears here, the analogous quantities for the whole populations (\hat{V}_1 and \hat{V}_2) were used in Section 5.2.3. Second, as here we considered robustness with respect to ΔK , the dependence on ΔK is different from the one in Section 5.2.3.

These differences notwithstanding, the intuitive meaning of the robustness measure (5.52) is the same as of ρ in Section 5.2.3: the species must differ both in their fluctuation-maintaining effect and their sensitivities towards fluctuations. The differential approach here has the advantage of implementing the model-independent connection between robustness and niche segregation (Meszéna et al., 2006).

5.5.2 Robustness of coexistence

Here we demonstrate the loss of robustness of coexistence when the two species becomes similar. For this purpose the simplified model is rewritten as

$$\frac{d}{dt}n_1(t) = \left[\mu\sigma\xi(t) - a(n(t) - K_1) - \mu b(n(t) - K_1)^2 \right] n_1(t), \quad (5.53)$$

$$\frac{d}{dt}n_2(t) = -a(n(t) - K_2)n_2(t), \quad (5.54)$$

where μ is the parameter measuring dissimilarity. The two species are identical for $\mu = 0$ and become dissimilar with increasing μ . The robustness of coexistence is determined by varying the carrying capacities.

Fig. 5.7 plots the ratio of the parameter region $(K_1, K_2) \in [0, 0.3] \times [0, 0.3]$, which allows coexistence, as a function of μ . Observe that robustness is lost gradually when the species become more and more similar. Coexistence becomes structurally unstable for $\mu = 0$, when only the case $K_1 = K_2$ supports coexistence.

This result, which is in line with theoretical expectations, is comparable with Fig. 6.4-6.6 of May (1973), or with Figs. 4.3 and 4.4.

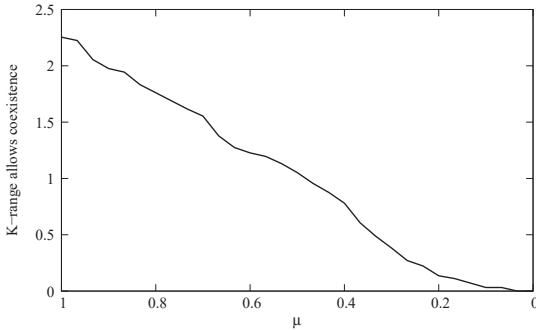


Figure 5.7: *Robustness of coexistence as a function of similarity. The vertical axis is the ratio of the parameter region $(K_1, K_2) \in [0, 0.3] \times [0, 0.3]$ allowing coexistence in arbitrary units. Parameters: $a = 0.1$; $b = 0.1$; $\sigma = 0.1$, the extinction limit $LIM = 10^{-40}$.*

5.6 Discussion

We aimed at studying the simplest possible model of fluctuation-mediated coexistence as deeply as possible in the context of a mathematical niche theory discussed in the previous chapters and Parvinen and Meszéna (2009). In line with this approach, simplicity is measured by the number of regulating variables. As a single regulating factor cannot support coexistence, we constructed a model with two of them (see Kisdi and Meszéna, 1993 for the original version). While all “strategic” (Czárán, 1998, p. xii) model studies pay a price in terms of realism, our sacrifice turned out to be higher than usual. The coexistence, which is maintained in our model in the infinite population size limit, requires astonishingly large population sizes. Its practical irrelevance notwithstanding, our model provided a test-bed for developing moment-closure treatment of problems and developing niche analyses in line with our theoretical context. The model supported the idea that sufficient niche differentiation with respect to the way populations are regulated is the requirement for robust coexistence in an environment that displays stationary fluctuations — just like in a constant one.

There are two distinct sources of stochasticity in population dynamics: environmental noise and demographic stochasticity (Case, 2000, p. 30). While both of them are present in almost any real ecological situation, it is meaningful to consider the approximations under which either or both of them are negligible. Demographic stochasticity is the more difficult problem. Neglecting it is equivalent to assuming infinite population size, i.e. describing population dynamics in terms of a continuous density variable. In this case, even if environmental noise is present, the dynamics is deterministic at least in the conditional sense, i.e. for a given realization of the environmental process. In contrast, finite population size and the unavoidable nature of demographic stochasticity makes analytical treatment with sufficient generality impossible beyond density-independent growth (cf. branching process theory, Haccou et al., 2005).

Classical coexistence theory was conceived in the context of the Lotka–Volterra model, disregarding both kinds of stochasticity. The resulting picture was simple and in line with biological intuition: coexistence is based on ecological niche differentiation leading to reduced interspecific competition and rare species advantage (Case,

2000, p. 368). However, as no clear lower bound of similarity was found (Abrams, 1983), further model studies blurred this simplicity. Strength of competition and niche have become terms of unclear meaning, terms to be defined separately in every specific situation.

The goal of Mesz  na et al. (2006) was to reestablish the intuitive as well as the mathematical clarity of coexistence theory on the general, model-independent level. Competition coefficients were defined differentially, therefore they became independent of the assumption of linearity in the Lotka–Volterra model. Niche was defined as the species’ differential impact on, and differential sensitivity towards the regulating variables, a generalization of the concept of the resource utilization function. Clear general connection between niche segregation and the robustness of coexistence was established on this basis. It was asserted that complications like population structure and environmental fluctuations can be tackled within this framework via time-scaling arguments (Mesz  na et al., 2006). The theory was extended for structured populations in a constant environment (see Chapters 3 and 4). The goal of this study was to apply the same framework for the minimal model of fluctuation-maintained coexistence.

In the limit of infinite population size it is self-evident that mutual invasion implies long-term coexistence; numerical experimentation with our model supported this principle unequivocally. Moreover, we were also able to determine the impact/sensitivity niche vectors and demonstrate their stated connection to the robustness of coexistence. While the analytical calculations were possible only via moment closure (valid for small fluctuations only), the construction itself is independent of this approximation.

Our analysis supported the insight shared by many (e.g. Abrams, 1983; Chesson, 1991) that coexistence in a fluctuating environment is not fundamentally different from the constant environment case. Fluctuations may contribute to opportunities for niche-segregation, but do not alleviate the necessity of ecological differentiation. The analogy between coexistence maintained by fluctuations and by resource heterogeneity operates on the mechanistic level. It is required for coexistence that the species which causes larger fluctuations in the total density is stronger in its sensitivity towards the fluctuations as well, relative to its dependence on the average total density. Similarly, the species depleting a specific resource more than

its competitor must depend on that specific resource more strongly to establish a coexistence-stabilizing rare advantage. In either case, increasing similarity weakens the stabilizing effect and reduces the robustness of coexistence. Robust coexistence requires dissimilarity both in the impacts on and the sensitivity towards the regulating variables. Note the similar conclusions of other models of fluctuation-mediated coexistence. Parvinen and Meszéna (2009) studied the case of repeated local catastrophes, while Barabás et al. (in prep.) investigated periodic environments.

While environmental stochasticity may have a diversity-maintaining effect, demographic stochasticity is invariably detrimental for coexistence. Any population with bounded population size is destined to extinction with probability 1 in infinite time. Mutual invasibility has the tendency to increase the time-span of coexistence, but it cannot prevent the eventual extinction. When the environment-driven stochasticity of the populations is relatively small, it remains true that mutual invasibility (and the niche-segregation behind it) may be able to maintain coexistence on a biologically relevant time-scale. However, as our example shows, the interaction between environmental and demographic stochasticity may lead to large fluctuations that makes the diversity-stabilizing effect of mutual invasibility irrelevant. Therefore, we should caution against the uncritical use of mutual invasibility as a sufficient condition for coexistence.

It is interesting to note that in case of a spatially extended population, *local* finiteness leads to a comparable importance of demographic stochasticity even in an infinite population (Oborny et al., 2005, 2007), which is also detrimental to coexistence (Mágori et al., 2005).

The extremely large density-fluctuations experienced in this model are presumably related to the low-frequency end of the white-noise spectrum. Extremely low densities are consequences of unfavorable environmental conditions experienced for extended periods of time. Therefore we may conjecture that a similar model with a different noise spectrum, while complicates the analytic treatment and increases the number of parameters, will turn out to be a more realistic description of fluctuation-mediated coexistence.

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Appendix A

Perron–Frobenius for continuous dynamics

In this appendix we discuss some technical differences between the continuous and discrete time formalisms of matrix populations.

Matrix population models are usually formulated in discrete time and Perron–Frobenius theorem plays a very important role in the discrete-time matrix population theory (Caswell, 2001, p. 79). Here we summarize the differing technicalities for continuous time and a proof of the “continuous” Perron–Frobenius theorem.

First of all, we should point out the difference in the definition of the “dominant” eigenvalue. For the purpose of matrix population modeling, the dominant eigenvalue is the one that describes the long-term population growth. As Eq. (1.20) demonstrates, the eigenvalue with the greatest real part plays this role in continuous time. In contrast, the long term behavior of the discrete-time matrix dynamics

$$\mathbf{n}_{t+1} = \mathbf{M}\mathbf{n}_t \tag{A.1}$$

is determined by the eigenvalue with the greatest *magnitude* (Caswell, 2001, p. 84).

In both cases, the simple long-term behavior of the population depends on the validity of the following two *Statements*:

- The dominant eigenvalue is real, unique and simple, i.e. the corresponding left and right eigenvectors are unique.
- The left and right eigenvectors, corresponding to the dominant eigenvalue, are real and strictly positive.

In discrete time, the biological interpretation requires the elements of the dynamical matrix \mathbf{M} to be non-negative. Then, together with the usual assumption of irreducibility and primitivity, the *Statements* are implied by the Perron–Frobenius theorem (cf. Caswell, 2001, p. 79).

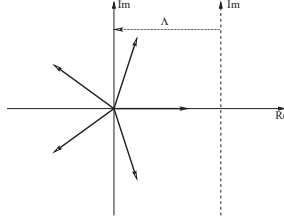


Figure A.1: *Eigenvalues with the greatest magnitude in an imprimitive matrix with $d = 5$.*

For continuous time the diagonal elements must be allowed to be negative. Still, as explained in Section 1.1.2, non-negativity holds for all off-diagonal elements in a biologically meaningful model. Non-negativity of the off-diagonals is also a consequence of the requirement that abundance of the i -states must remain non-negative under all circumstances.¹ Irreducibility of the matrix is assumed again, primitivity will not be needed.

Proof of the Statements One can chose a positive real positive constant Λ such that the matrix

$$\mathbf{M}^+ = \mathbf{M} + \Lambda \mathbf{1} \quad (\text{A.2})$$

is nonnegative. Matrix \mathbf{M}^+ inherits irreducibility from matrix \mathbf{M} . Perron–Frobenius theorem applies for \mathbf{M}^+ and guaranties, that there exists a real positive eigenvalue ρ_1^+ , that has the greatest magnitude and is simple; the corresponding left and right eigenvectors are real and strictly positive. Obviously, ρ_1^+ can be characterized as the eigenvalue of matrix \mathbf{M}^+ with the greatest real part (Fig. A.1). Matrix \mathbf{M} has the

¹Assume, that $M_{ij} < 0$ for any $i \neq j$ and only n_j is different from zero. Then, the resulting $dn_i/dt < 0$ would be absurd.

very same eigenvectors as of \mathbf{M}^+ , but its eigenvalues are shifted by the real constant $-\Lambda$. Obviously, the eigenvalue of matrix \mathbf{M} with the greatest real part is

$$\rho_1 = \rho_1^+ - \Lambda, \tag{A.3}$$

which proves the statements.

Note that ρ_1 is not necessarily the eigenvalue of the greatest magnitude of matrix \mathbf{M} . As the matrix \mathbf{M}^+ is allowed to be imprimitive, it may have additional eigenvalues with the same magnitude as ρ_1^+ . Still, ρ_1^+ and ρ_1 are unique in their capacity of being the eigenvalue (of the corresponding matrix) with the greatest real part. In discrete time, imprimitivity with imprimitivity index d would result in periodic behavior with period d . No such issue exists in real time. Therefore, while primitivity is a usual assumption in discrete time, it is not needed for the continuous case.

Appendix B

Perturbation of growth rate and population structure

Here we derive Eqs. (3.11–3.12) by determining the perturbation of the growth rate r and population structure \mathbf{p} of any population under a small change $d\mathbf{M}$ of the dynamical matrix \mathbf{M} .

The perturbed quantities will be denoted by prime. The perturbed eigenvalue equation is

$$\mathbf{M}'\mathbf{p}' = \rho'_1\mathbf{p}', \quad (\text{B.1})$$

where

$$\mathbf{M}' = \mathbf{M} + d\mathbf{M} \quad (\text{B.2})$$

is the perturbed dynamical matrix.

We want to express the perturbed population structure \mathbf{p}' in terms of the unperturbed right eigenvectors of the matrix \mathbf{M} , as

$$\mathbf{p}' = \sum_{j=1}^D c_j \mathbf{w}_j, \quad (\text{B.3})$$

where c_j are coefficients to determine.¹ Substitution into Eq. (B.1) leads to

¹It is always possible, if the matrix has D different eigenvectors, i.e. if it is of simple structure.

$$(\mathbf{M} + d\mathbf{M}) \sum_j c_j \mathbf{w}_j = \varrho'_1 \sum_j c_j \mathbf{w}_j. \quad (\text{B.4})$$

We multiply this equality with the dominant left eigenvector \mathbf{v}_1 from the left and use the orthogonality relation (1.22).

$$\sum_j c_j \mathbf{v}_1 d\mathbf{M} \mathbf{w}_j = (\varrho'_1 - \varrho_1) c_1. \quad (\text{B.5})$$

By Eq. (1.25), vanishing perturbation corresponds to $c_1 = 1$. Then, one can write

$$c_1 = 1 + dc_1 + \text{h.o.t.}, \quad (\text{B.6})$$

where dc_1 is proportional to the perturbation; the higher order terms are omitted. The rest of the coefficients vanish without the perturbation, so

$$c_j = dc_j + \text{h.o.t} \quad j \neq 1. \quad (\text{B.7})$$

With substitution of these forms into Eq. (B.5) and omission of the higher order terms one arrives to the change of the growth rate

$$dr = d\varrho_1 = \varrho'_1 - \varrho_1 = \mathbf{v}_1 d\mathbf{M} \mathbf{w}_1 = \mathbf{v} d\mathbf{M} \mathbf{p}, \quad (\text{B.8})$$

where the notations $\mathbf{v} = \mathbf{v}_1$, $\mathbf{p} = \mathbf{w}_1$ were used (cf. Caswell, 2001, p. 209).

Now we turn to determine the perturbation of the population structure. Eq. (B.4) is multiplied with \mathbf{v}_i ($i \neq 1$) from the left, leading to

$$\sum_j c_j \mathbf{v}_i d\mathbf{M} \mathbf{w}_j = (\varrho'_1 - \varrho_i) c_i. \quad (\text{B.9})$$

Using Eq. (B.7) results in

$$dc_i = \frac{\mathbf{v}_i d\mathbf{M} \mathbf{p}}{\varrho_1 - \varrho_i} \quad i \neq 1. \quad (\text{B.10})$$

Then the perturbed population structure is

$$\mathbf{p}' = (1 + dc_1) \mathbf{p} + \sum_{i \neq 1} \frac{\mathbf{v}_i d\mathbf{M} \mathbf{p}}{\varrho_1 - \varrho_i} \mathbf{w}_i. \quad (\text{B.11})$$

The value of dc_1 is determined by the requirement of preserving the summation the elements of \mathbf{p} :

$$1 = \sum_{l=1}^s p'_l = 1 + dc_1 + \sum_{i \neq 1} dc_i U_i, \quad (\text{B.12})$$

where U_i was defined by Eq. (3.13). This leads to

$$dc_1 = - \sum_{i \neq 1} dc_i U_i. \quad (\text{B.13})$$

Then, from Eq. (B.3),

$$d\mathbf{p} = \mathbf{p}' - \mathbf{p} = dc_1 \mathbf{p} + \sum_{i \neq 1} dc_i \mathbf{w}_i. \quad (\text{B.14})$$

Substituting this into Eq. (B.11) leads to

$$d\mathbf{p} = \sum_{i \neq 1} \frac{(\mathbf{w}_i - U_i \mathbf{p}) \circ \mathbf{v}_i}{\varrho_1 - \varrho_i} d\mathbf{M} \mathbf{p}, \quad (\text{B.15})$$

which can be written into the form (3.11) by introducing the matrix \mathbf{A} with (3.12).

Appendix C

Derivation of the analytic formulae of the niche vectors

The dynamical matrix of the two patch system described in Section 4.2.1 is the following (cf. Eq. (4.4))

$$\mathbf{M}^{(i)} = \begin{pmatrix} r_{0A}^{(i)} - \alpha I_A - \mu & \mu \\ \mu & r_{0B}^{(i)} - \alpha I_B - \mu \end{pmatrix}. \quad (\text{C.1})$$

The regulating variables collected into the vector \mathbf{I} ($j = A, B$)

$$I_j = \sum_i n_j^{(i)}. \quad (\text{C.2})$$

The 2×2 symmetrical dynamical matrix $\mathbf{M}^{(i)}$ has two real eigenvalues: ρ^+ (the dominant eigenvalue) and $\rho^- < \rho^+$. We can express the left and right dominant eigenvectors of species i with the number of individuals in the patches

$$\mathbf{p}^{(i)} = \frac{1}{n_A^{(i)} + n_B^{(i)}} \begin{pmatrix} n_A^{(i)} \\ n_B^{(i)} \end{pmatrix}, \quad \mathbf{v}^{(i)} = \frac{n_A^{(i)} + n_B^{(i)}}{\left(n_A^{(i)}\right)^2 + \left(n_B^{(i)}\right)^2} \begin{pmatrix} n_A^{(i)} \\ n_B^{(i)} \end{pmatrix}, \quad (\text{C.3})$$

where we used the normalization introduced by Eqs. (1.16) and (1.22). The eigenvectors correspond to ρ^- are the following

$$\mathbf{w}_2^{(i)} = \mathbf{v}_2^{(i)} = \frac{1}{\sqrt{\left(n_A^{(i)}\right)^2 + \left(n_B^{(i)}\right)^2}} \begin{pmatrix} -n_B^{(i)} \\ n_A^{(i)} \end{pmatrix}. \quad (\text{C.4})$$

To compute the sensitivity vector of species i , we should determine operator $T_{jkm}^{(i)}$ describes the connection between the dynamical matrix and the regulating variables. From Eqs. (3.4) and (C.1) we get

$$T_{jkm}^{(i)} = \alpha \delta_{jkm}, \quad (\text{C.5})$$

where $\delta_{jkm} = 1$ if $j = k = m$, zero otherwise.

From Eq. (3.7) the derivation of the sensitivity niche vectors is straightforward, the result is

$$\mathbf{S}^{(i)} = \frac{\alpha}{\left[\left(n_A^{(i)} \right)^2 + \left(n_B^{(i)} \right)^2 \right]} \begin{pmatrix} \left(n_A^{(i)} \right)^2 \\ \left(n_B^{(i)} \right)^2 \end{pmatrix}. \quad (\text{C.6})$$

As a first step to get the analytical form of the impact niche vector we should find matrix \mathbf{A} describes the correction to the equilibrium distribution. A direct calculation using the proper form of Eq. (3.12)

$$\mathbf{A}^{(i)} = \frac{(\mathbf{w}_2^{(i)} - U_2^{(i)} \mathbf{p}^{(i)}) \circ \mathbf{v}_2^{(i)}}{\rho_1^{(i)} - \rho_2^{(i)}}, \quad (\text{C.7})$$

after a long computation leads to the following result

$$\mathbf{A}^{(i)} = \frac{1}{\Delta \rho^{(i)}} \frac{1}{n_A^{(i)} + n_B^{(i)}} \begin{pmatrix} n_B^{(i)} & -n_A^{(i)} \\ -n_B^{(i)} & n_A^{(i)} \end{pmatrix}. \quad (\text{C.8})$$

From Eq. (3.17) using Eqs. (3.23) and (C.5)

$$\mathbf{H} = \begin{pmatrix} G & -G \\ -G & G \end{pmatrix}, \quad (\text{C.9})$$

where

$$G = \sum_i \frac{\alpha}{\Delta \rho^{(i)}} \frac{n_A^{(i)} n_B^{(i)}}{n_A^{(i)} + n_B^{(i)}}. \quad (\text{C.10})$$

As a final step, from the definition of Eq. (3.18) the impact niche vectors are

$$\mathbf{C}^{(i)} = (\mathbf{1} + \mathbf{H})^{-1} \mathbf{F}^{(i)} \mathbf{p}^{(i)} = \frac{1}{2G+1} \left[\frac{1}{n_A^{(i)} + n_B^{(i)}} \begin{pmatrix} n_A^{(i)} \\ n_B^{(i)} \end{pmatrix} + G \begin{pmatrix} 1 \\ 1 \end{pmatrix} \right]. \quad (\text{C.11})$$

Appendix D

Stratonovich and Itô interpretation of stochastic dynamics

In handling a white noise in Chapter 5 caution is needed in defining a “stochastic” integral, like

$$\int g(t)\xi(t)dt = \int g(t)dW(t), \quad (\text{D.1})$$

where $\xi(t)$ is the white noise. Here $W(t)$ denotes the Wiener process, the derivative of which is the white noise:

$$dW = \xi dt. \quad (\text{D.2})$$

Note that

$$\overline{(dW)^2} = dt, \quad (\text{D.3})$$

a quite nontrivial feature of the white noise.

Then, integral (D.1) can be approximated by two different sums, referred to as “Stratonovich” and “Itô” type – here we use function notation instead of indices

$$(\mathcal{S}) \quad \sum_l \frac{g(t_{l+1}) + g(t_l)}{2} \Delta W(t_l) \quad (\text{D.4})$$

$$(\mathcal{I}) \quad \sum_l g(t_l) \Delta W(t_l) \quad (\text{D.5})$$

(Δ means difference between values at t_{l+1} and t_l). The difference between the two sums is

$$(\mathcal{S} - \mathcal{I}) \quad \sum_l \frac{1}{2} \Delta g(t_l) \Delta W(t_l). \quad (\text{D.6})$$

Were g and W smooth functions, each term of (D.6) would be proportional to $(\Delta t)^2$ and the difference between the two approximations would disappear in the limit $\Delta t \rightarrow 0$. However, because of the property (D.3), if Δg is proportional to ΔW , then the expectation of a term is proportional to $\overline{(\Delta W)^2} = \Delta t$. Then, the difference $(\mathcal{S} - \mathcal{I})$ remains finite in the limit; the sums (\mathcal{S}) and (\mathcal{I}) converge to two different values. These two limits constitute two different definitions of the stochastic integral (D.1). For stochastic differential equations (SDE) the two different ways of integration establishes two different solutions, i.e. two inequivalent interpretations of the SDE.

If one describe a continuous process in the limit of zero correlation time the Stratonovich-interpretation is the correct one; Itô can be used only after proper re-definition of the terms. During a time step, the noise should be weighted by the *average* of the quantity g during that time step. Bored by the growing volume of the Itô–Stratonovich literature, Smythe et al. (1983) established the validity of the Stratonovich approach for describing continuous stochastic phenomena *experimentally*. They observed also that the naive numerical discretization, corresponding to the Itô-interpretation, leads to an incorrect result.

Consider now the discretization of our model defined by the SDE (1.17). Naively, one would arrive at the iteration

$$n_{i,t+\Delta t} - n_{i,t} = [-a_i(n_t - K_i) - b_i(n_t - K_i)^2] n_{i,t} \Delta t + \sigma_i n_{i,t} \sqrt{\Delta t} \xi_t. \quad (\text{D.7})$$

(The factor $\sqrt{\Delta t}$ ensures compliance with Eq. (D.3) when the i.i.d. ξ_t has a variance 1.) However, the $\Delta t \rightarrow 0$ limit of this iteration would lead to the Itô, instead of the Stratonovich-interpretation of the stochastic dynamics (1.17). One has to take into account the correction (D.6).

Only the stochastic term of the iteration (D.7) is of interest. Then $\Delta W(t)$ corresponds to $\sqrt{\Delta t} \xi_t$ and $g(t) = \sigma_i n_{it}$; therefore $\Delta g(t_i) = \sigma_i \Delta n_i(t_i)$. However,

$$\Delta n_i(t_i) = \sigma_i n_i(t_i) \Delta W(t_i) \quad (\text{D.8})$$

by the iteration; only the stochastic term was taken into account. Therefore,

$$\Delta g(t_i) = \sigma_i^2 n_i(t_i) \Delta W(t_i) \quad (\text{D.9})$$

and a term in the correction (D.6) reads as

$$\frac{1}{2} \sigma_i^2 n_i(t_i) (\Delta W(t_i))^2 = \frac{1}{2} \sigma_i^2 n_i(t_i) \Delta t. \quad (\text{D.10})$$

The expectation value of this correction leads to the correction term $\frac{1}{2}\sigma_i^2\overline{n}_i$ in the iteration (5.24).

We proceed to prove Eq. (5.30); Eq. (5.37) is analogous. Averaging is defined via integration, so the considerations above apply. The Itô average of the product $m\xi$ is zero: value of m in each time step depends only on the values of ξ of the previous steps, which is independent from the current ξ . Therefore the Stratonovich average $\overline{m\xi}$ comes entirely from the Stratonovich-Itô correction. As now $g(t)$ corresponds to $m(t)$ and $\Delta m = \Delta n$, Eq. (D.8) leads to the relation (5.30).

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Összefoglalás

Doktori dolgozatom alapja az ökológiai rendszerek leírásának egyik – sokszor használt, de nem egységesen definiált – kulcsfogalma: a niche. Vizsgálataink keretét Meszéna és munkatársai (2006) által bevezetett modell-független niche fogalma képezi, amely egy populáció ökológiai szerepét két részre bontja: hogyan függ egy populáció a növekedése a reguláló tényezőktől (szenzitivitás niche), és hogyan függnek a reguláló tényezők a populáció létszámától (impakt niche). Megmutatták, hogy robusztus – a külső környezet paramétereinek változását tolerálni képes – együttélés csak akkor jöhet létre, ha a fajok a reguláló tényezőktől való függésükben és azokra való hatásukban (szenzitivitásukban és impaktjukban) is megfelelően különböznek, valamint, hogy az együtt élő fajok hasonlóságának nincsen alsó korlátja, azonban a hasonlóság növekedésével az együttélés egyre érzékenyebb lesz a környezet változására. Munkánkban a fenti, homogén populációkra bevezetett niche fogalmat terjesztettük ki strukturált populációkra, valamint vizsgáltuk alkalmazhatóságát fluktuáló környezetben együtt élő populációk leírására, elősegítve ezzel az elmélet valós ökológiai szituációkban való használhatóságát. A bevezetett niche-modell segítségével mind tetszőleges strukturált populációra, mind időben fluktuáló környezetre beláttuk, hogy az együttélésre képes fajok hasonlóságának nincs alsó korlátja, az együttélés robusztusságát az impakt és szenzitivitás niche vektorok lineáris függetlenségének mértéke határozza meg. Két foltból álló modell-környezetben analitikusan kimutattuk a niche-szegregációt: a fundamentális és a realizált niche különbségét, valamint az adaptív dinamika eszközkészletével megmutattuk, hogy a térbeli heterogenitás fenn tud tartani genetikai polimorfizmust; evolúciós elágazás következhet be, akár a foltok közötti migráció csökkenésével, akár a foltok közötti különbség növekedésével. Megmutattuk, hogy a fajok között fennálló „relatív nemlinearitás” esetén a környezeti fluktuáció hatására több faj élhet együtt, mint stabil környezet mellett. Kimutattuk hogy az együttélés feltételének tekintett kölcsönös invazibilitás sztochasztikusan fluktuáló környezetben csak végtelen populációméret mellett igaz, véges populációkra nem alkalmazható.

Summary

This dissertation is based on the concept of niche, which is one of the – frequently used but not consistently defined – key concepts of ecology. The framework of our investigations is based on the model-independent niche concept introduced by Meszén et al. (2006). It decomposes the ecological role of a given population into two parts: how does the growth rate depend on regulating factors (sensitivity niche), and how does the regulating factors depend on the number of the individuals (impact niche). We showed, that robust coexistence is possible only if the species are different enough in their dependence of, and effect on, the regulating factors (i.e. different enough in both sensitivity and impact niches). We also demonstrated that there is no lower bound of similarity between coexisting species, merely with increasing similarity the sensitivity of the coexistence becomes higher towards to the external environmental parameters. In our work we extended this niche concept introduced for homogeneous populations to structured populations, and investigated its applicability to describing coexisting populations in fluctuating environment. This promotes the applicability of this theory in real ecological scenarios. By the means of the introduced niche-model we proved for both structured populations and fluctuating environment, that there is no lower bound of similarity of coexisting species, and the robustness of coexistence is determined by the measure of the linear dissimilarity of impact and sensitivity niche vectors. In a two-patch model environment we showed analytically the phenomenon of niche-segregation: the difference between the fundamental and realized niches; and by the means of adaptive dynamic we showed that polymorphism can be maintained by spatial heterogeneity, evolutionary branching can occur due to either decreasing migration or increasing difference between the patches. By investigation of a minimal model we confirmed that in case of “relative nonlinearity” among species more species can coexist as a result of (uncorrelated) environmental fluctuation. We demonstrated that in stochastically fluctuating environment the mutual invasibility considered necessary condition of coexistence is valid only in case of infinitely large populations, and not applicable in all cases for finite populations.